1989

Ecological Consequences of Variation in Pollinator Availability: Ocotillo, Carpenter Bees, and Hummingbirds in Two Deserts.

Peter Evans Scott
Louisiana State University and Agricultural & Mechanical College

INFORMATION TO USERS

The most advanced technology has been used to photograph and reproduce this manuscript from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book. These are also available as one exposure on a standard 35mm slide or as a 17" x 23" black and white photographic print for an additional charge.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

U·M·I

University Microfilms International
A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
313/761-4700 800/521-0600

Order Number 9017291

Ecological consequences of variation in pollinator availability: Ocotillo, carpenter bees, and hummingbirds in two deserts

Scott, Peter Evans, Ph.D.

The Louisiana State University and Agricultural and Mechanical Col., 1989

U·M·I

300 N. Zeeb Rd.
Ann Arbor, MI 48106

ECOLOGICAL CONSEQUENCES OF VARIATION IN POLLINATOR AVAILABILITY: OCOTILLO, CARPENTER BEES, AND HUMMINGBIRDS IN TWO DESERTS

A Dissertation
Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of

Doctor of Philosophy

in

The Department of Zoology and Physiology

by
Peter Evans Scott
B. A., Yale University, 1973
M. A., The University of Texas at Austin, 1984
August 1989

ACKNOWLEDGMENTS

I am grateful to Dr. J. V. Remsen, my major professor, for constant encouragement and support, for teaching me much about ornithology and ecology, and for help with field work in Texas. I also thank the other members of my committee for their time in reviewing proposals and the dissertation: Dr. David Foltz, Dr. Mark Hafner, Dr. D. G. Homberger, Dr. G. B. Williamson, Dr. Lowell Urbatsch, and Dr. Robert Nauman.

The foundation for a study of *Fouquieria splendens* was laid by James Henrickson and Nickolas Waser. Both men commented helpfully on proposals and strongly encouraged my research. Much of what I have learned about pollination ecology is due to the thoughtful criticisms of Nick Waser and the example of his work.

I thank the National Park Service for permission to conduct research in Big Bend National Park, and for providing convenient living quarters at "KBar". I am especially grateful to park biologist Mike Fleming. Many other friends on the park staff were supportive, including John and Tina Pearson, Anne and Jim Bellamy, and Cindy and Richard Simmons. I thank Anne Bellamy for keeping me posted on the flowering of ocotillo.

The staff of Anza-Borrego Desert State Park was also helpful. Mark Jorgensen suggested excellent study sites. He and Bob Theriault shared their knowledge of desert natural history. Pat and Lola Gene Barden and Manfred Knaak were generous hosts at Tamarisk Grove campground.

Mike Powell and Richard Hilsenbeck of Sul Ross State University educated me on the botany of trans-Pecos Texas. I am grateful to Richard for opening his lab to me and for loaning a microscope. Nancy Newfield instructed me in the arts of capturing and

marking hummingbirds. Mahlon Ayme was a valuable field assistant. Catherine Cummins, Tina Pearson, and Marian Scott sewed pollination bags. Cheryl Barr of the L.S.U. Entomology Collection loaned supplies and curated bees. She, Mike Israel, and Tim Friedlander identified insects.

Financial support was provided by a fellowship from the Alumni Federation of Louisiana State University, and by funds from the Museum of Natural Science and the Department of Zoology and Physiology. Additional support came from Sigma Xi, the Scientific Research Society, from The Frank M. Chapman Fund (American Museum of Natural History), and from the Texas Ornithological Society.

I thank my parents, Marian F. Scott and William E. Scott, for their generous support of my graduate education.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

I studied the pollination ecology of a widespread desert shrub, ocotillo (*Fouquieria splendens*), and some of the consequences of geographic variation in availability of pollinators. I studied ocotillo in the Chihuahuan Desert of western Texas (Big Bend National Park) for three flowering seasons, and in the Sonoran Desert of southern California (Anza-Borrego Desert State Park) for parts of two flowering seasons. In both areas, ocotillo flowers profusely for one month each year, and requires outcross pollination to mature more than 5% of its potential seed crop.

In Texas, carpenter bees (*Xylocopa californica arizonensis*) and their nest plants (species of *Agave, Dasylirion*, and *Yucca*) are common throughout the habitats occupied by ocotillo, whereas hummingbirds (*Calothorax lucifer, Archilochus alexandri*) have localized distributions. In two of three years, carpenter bees thoroughly harvested the nectar and pollen of ocotillo, resulting in high fruit set and seed set. Female carpenter bees provisioned spring nests with pollen from *F. splendens* and mesquite (*Prosopis glandulosa*) and with nectar sugar; *F. splendens* accounted for 69% of pollen volume in an average nest. Ocotillo's direct contribution to carpenter bee fecundity and an abundance of nest plants help maintain a high bee density in Texas.

In California, carpenter bees nest only in palms (*Washingtonia filifera)* and are unavailable to many ocotillo populations. Costa's Hummingbird (*Calypte costae*) is widespread, and migrant Rufous Hummingbirds (*Selasphorus rufus*) and orioles (*Icterus* spp.) are sometimes common. Ocotillo populations were poorly pollinated and only a small percentage of their nectar was harvested, except during a brief period when migrant hummingbirds were abundant. Density of breeding Costa's Hummingbirds is much lower than the March nectar supply would support. Two aspects of hummingbird

biology may be responsible for the disparity: a low reproductive rate, and high daily energy requirements throughout the year.

Ocotillo is engaged in a strong mutualism with carpenter bees in Texas, but interacts weakly with hummingbirds and orioles in California. This suggests that biological idiosyncrasies of flower-visiting animals are important in determining whether interactions between plants and potential pollinators become effective mutualisms.

Chapter 1

Introduction

Many plants that rely on animal pollinators attract more than one effective pollinator and experience variation in the relative abundance of pollinator species. Changes may occur during a flowering season (Waser and Price 1981, Paige and Whitham 1985), between years (Waser 1979), or over a geographic or altitudinal range (Armbruster 1985, Galen 1985). When availability of pollinator species varies geographically in a consistent way, populations of a plant may adapt to local conditions, because pollination success is an important component of fitness. Gene flow through pollen and seed dispersal is often restricted (Waser and Price 1983), making it possible for floral characters favored by local selection pressures to increase in frequency. This has occurred, for example, in *Polemonium viscosum*: a "skunky" floral scent is favored in habitats where flies are the common pollinator and a sweet scent at higher elevations, where bumblebees predominate (Galen 1985).

Whether or not local adaptation occurs, geographic variation in pollinator availability may have interesting ecological consequences. It can affect the character of plant-pollinator mutualisms: how effectively and reliably a plant is pollinated, and how large an effect its rewards have on its pollinator(s). Floral rewards are usually food in the form of pollen (a protein source) or nectar (a sugar-rich energy source, sometimes rich in amino acids or nutrients) (Simpson and Neff 1983). Depending on the pollinator's biology, the food may be used to offset daily energy expenditures or to feed young, for a brief part of the life cycle or for much of it (Gilbert 1977, Addicott 1986). Thus a plant may or may not exert a large effect on pollinator density, which in turn can influence the rate of visitation to its flowers. Pollinator density may be limited by factors other than food supply, such as habitat for nesting or predation rates. And

although actual density is important, vistation rates are influenced by other plant species that flower simultaneously and compete for a pollinator's services (Waser 1978), and by competing nectarivores that alter plant reward levels (McDade and Kinsman 1980) or defend them (Roubik 1982). Any of these factors may vary over a plant's range.

Plants with broad geographic ranges are likely to experience such variation in pollinator availability. The desert shrub ocotillo, *Fouquieria splendens* (Fouquieriaceae), has a broad distribution in deserts of the southwestern United States and northern Mexico. It occurs in the northern two-thirds of the Sonoran Desert and throughout the Chihuahuan Desert. [See Henrickson (1972: 511, Fig. 23) for the range of *F. splendens*; Turner and Brown (1982: 189, Fig. 113) for the Sonoran Desert; Schmidt (1986: Fig. 1) for the Chihuahuan Desert.] In many desert scrub and semi-desert grassland communities, *F. splendens* is one of the dominant woody perennials (Simpson 1977, Turner and Brown 1982). It flowers profusely in spring, when it produces several hundred to several thousand red tubular flowers in two to four weeks. An average flower produces 1-4 mg of nectar sugar and 3-4 mg pollen (Chapters 2, 3; Simpson 1977, Waser 1979). Rich floral rewards, massive flowering, abundance, and longevity make ocotillo one of the most productive desert perennials in terms of floral rewards (Simpson 1977).

Waser (1979) showed that *F. splendens* has two major pollinators at Tucson, Arizona: migrant hummingbirds (primarily *Archilochus alexandri*) and a carpenter bee (*Xylocopa californica arizonensis*). Other studies (Grant and Grant 1968, Henrickson 1972) suggested that availability of these two pollinator types varied considerably across the range of *F. splendens*. Henrickson (1972) described geographic variation in floral traits that possibly reflects adaptation to different pollinators: mean length of the corolla tube decreases by approximately 6 mm from west to east, and stigma placement varies. These patterns led me to study the pollination ecology of ocotillo at two sites near

the eastern and western edges of the range: Big Bend National Park, Brewster County, Texas (29° N, 103° W), in the northern Chihuahuan Desert, and Anza-Borrego Desert State Park, San Diego County, California (33° N, 116° W), in the northwestern Sonoran Desert. The results can be compared with Waser's (1979) study at a geographically intermediate site in the eastern Sonoran Desert at Tucson (32° N, 111° W).

In both areas, I measured: (1) flower and nectar production; (2) the visitation rates of hummingbirds, carpenter bees, and other flower visitors; (3) the extent to which rewards were harvested; (4) pollination effectiveness; and I (5) tested ocotillo's breeding system. I also assessed the importance of ocotillo rewards for the primary pollinators, carpenter bees and hummingbirds, and identified other factors that affected their availability.

My aim has been to investigate the ecological consequences of ocotillo's interaction with different pollinators that occur at various densities. Do carpenter bees and hummingbirds differ in their effectiveness as pollinators of ocotillo? If so, is it because of density, energy requirements, foraging behavior, or the way in which floral parts are contacted? What are the effects of ocotillo's food rewards on bee and hummingbird populations?

My analysis leads to a consideration of one of the hypothesized attributes of plant-pollinator mutualisms: the tendency for pollinator populations to reach an equilibrium density at which floral rewards are completely harvested and pollination success is maximized (Montgomerie and Gass 1981). This should occur if pollinator populations are most directly limited by floral food rewards (Waser 1978). Genetic feedback within plant populations should favor complete use of floral rewards by effective pollinators (Montgomerie and Gass 1981). Nectar is costly, and production in excess of the amount necessary to attract pollinators might reduce a plant's seed output or survivorship. However, authors have recognized a number of situations which could keep floral reward levels and pollinator populations from equilibrating (Montgomerie

and Gass 1981, Waser 1983). Addicott (1986) points out that plants and pollinators provide only one type of service (food, or transfer of gametes) and are therefore likely to have a less profound effect on each other's population density than, for example, ants and acacias. The example of ocotillo and its pollinators is instructive for studying population-level effects of mutualism on pollinator species. As a common perennial that produces large quantities of nectar and pollen each spring, ocotillo is more capable than many plants of contributing to growth of a pollinator population. Its two major pollinators differ in the use they make of floral rewards and in their energetic requirements.

Evolutionary questions arise from the analysis of ocotillo-pollinator interactions. These concern the adaptive value of ocotillo's floral structure, phenology, and breeding system, and the question of whether local populations have adapted to particular pollinators. It is unlikely that coevolution, in a strict sense, has occurred between ocotillo and its pollinators. Futuyma and Slatkin (1983) define coevolution as having occurred "when, in each of two or more ecologically interacting species, there is adaptive response to genetic change in the other(s)." Adaptation by hummingbirds to particular flower species is exceptional, because hummingbirds feed daily throughout the year; most visit many different flower species (Feinsinger 1983). The only convincing case of coevolution involving a hummingbird of the United States is the evolution of winter breeding in Anna's Hummingbirds (*Calypte anna*) and winter flowering in *Ribes speciosum* (Stiles 1973). Adaptation to particular flower species is also unlikely for carpenter bee species, whose nectar-robbing ability gives them access to a variety of flower types. Adaptation by a plant to a particular pollinator or set of pollinators is more likely, because the pollinator(s) may visit reliably during most flowering periods, and an occasional failure in pollinator service is not disastrous for plants that flower repeatedly. Adaptation should occur "if some subset of all available visitors, taken together, provides a given plant with an optimal quality and quantity of

pollen transfer" (Waser 1983: 254). Because the genetic control of many floral characters is simple (Gottlieb 1984) and gene flow is often restricted, the potential for local adaptation to pollinators is high in plants. My discussion of adaptation by *F. splendens* is speculative and is partly based on consideration of the floral traits of other *Fouquieria* species (Henrickson 1972). Hypotheses of adaptation were not tested in this study.

The organization of this dissertation is as follows. In Chapters 2 and 3 I present the results of studies in Texas, and in Chapter 4 the California results. In Chapter 5 I summarize my conclusions and discuss the evolution of floral traits in *F. splendens*. In the remainder of this chapter I review the natural history of hummingbirds and carpenter bees, their distribution over the range of *F. splendens*, and Waser's (1979) study of the pollination ecology of *F. splendens* at Tucson.

Characteristics of hummingbirds and carpenter bees

Hummingbirds and carpenter bees, being members of different animal classes, differ in a number of ways that may affect their roles as mutualists of plants and as competitors for floral rewards. As specialized nectarivores they are also similar in many ways. Nectar is the only floral reward used by hummingbirds, which also consume arthropods regularly (Remsen et al. 1986). Most hummingbirds devote 90% or more of daily foraging time to harvesting nectar (Gass and Montgomerie 1981). Nectar is used in balancing daily energy expenditures, including the elevated costs of breeding and molt (Stiles 1979), and in building fat reserves during migration (Carpenter et al. 1983). Its importance as a food for nestlings is not known, but arthropods are definitely needed. Clutch size is two eggs and the breeding cycle lasts seven to eight weeks (including one to two weeks of fledgling dependence), limiting the advantage that can be taken from a short-term flush of floral resources. Maximum longevity is at least eight years (Calder et al. 1983). Daily energy expenditures of hummingbirds are high:

an estimated 31 kiloJoules for *Cynanthus latirostris* (weight: 3 g) (Montgomerie 1979), equivalent to the energy yield of 1.8 grams of sucrose. The high energy demand has a beneficial consequence for plants (one hummingbird may visit thousands of flowers per day), but it also means that a brief energy shortage can limit the density of a hummingbird population (Stiles 1979). Hummingbirds can reduce their metabolic rate by 50-90% by becoming torpid, but only for several hours at night (Hainsworth and Wolf 1970).

Carpenter bees are completely dependent on floral rewards, but are able to survive lean periods and to overwinter by building fat reserves (Louw and Nicolson 1983), becoming inactive, and greatly lowering their metabolic rate. The adult food is mainly nectar; females also consume pollen prior to egg-laying (Gerling and Hermann 1978). Large size prohibits carpenter bees from entering most tubular flowers, but specialized maxillae enable them to pierce the bases of flower tubes and "rob" nectar (Schremmer 1972). Each larva's food is a mixture of pollen and nectar gathered by a solitary female (or two) before the egg is laid. Brood size is variable (6-16 provisioned cells in *X. c. arizonensis*) and depends on the duration and abundance of floral resources. Young take approximately 50 days to develop and are vulnerable to predation by woodpeckers and parasitism by beefly and meloid beetle larvae (see Chapter 3 and Watmough 1983). Each carpenter bee species is dependent on a restricted set of nest plants, in which females excavate tunnels and both sexes overwinter (Hurd and Moure 1963). More than one breeding episode may occur in an intermittently active season of seven months. Generations overlap in survival and perhaps in breeding activity. Longevity is not well known, but it appears common for individuals to be active in at least parts of two years (Gerling and Hermann 1978).

Carpenter bees are similar to hummingbirds in being generalist nectarivores and having high daily energy expenditures when active (Chappell 1982). Both are strong fliers capable of foraging over ranges > 1 km in diameter, and are active from dawn to

dusk, temperatures permitting. Both harvest nectar quickly; hummingbirds average 1-2 seconds/flower and carpenter bees approximately 5 seconds/flower. However, carpenter bees can forage profitably when mean nectar rewards are less than 0.1 mg sugar/flower (Louw and Nicolson 1983), whereas hummingbirds apparently cannot: available nectar in Rufous Hummingbird territories rarely drops below 0.2 mg sugar/flower (Kodric-Brown and Brown 1978).

Distribution of hummingbirds, carpenter bees, and other nectar plants over the range of Fouquieria splendens

Hummingbirds are much more common in the western Sonoran Desert than in the Chihuahuan. Costa's Hummingbird (*Calypte costae*), "the dry desert hummingbird *par excellence* " (Phillips et al. 1964), occupies the outwash plains and desert scrub habitat of southwestern Arizona and southern California from February until May or June, and breeds during flowering of ocotillo. In addition, the northward migration of Rufous Hummingbirds (*Selasphorus rufus*), peaking in March and early April (Phillips et al. 1964, Garrett and Dunn 1981), is confined to the western Sonoran Desert and Pacific coastal habitats.

According to Grant and Grant (1968), ocotillo is "the chief source of nectar" for hummingbirds in spring in southeastern California and southwestern Arizona. Its closest rival would be chuparosa, *Justicia (Beloperone) californica*, a profusely flowering shrub common in washes that dissect the outwash plains (Daniel 1984). In this region *Fouquieria splendens* and *J. californica* together provide a stable supply of nectar for two or three months (February to April).

In the eastern Sonoran Desert at Tucson, Arizona, Costa's is uncommon and Rufous is rare in spring. Migrant Black-chinned (*Archilochus alexandri*) are the principal hummingbird visitors to ocotillo (Waser 1979).

In the Chihuahuan Desert, there is neither a widespread breeding hummingbird nor a common spring migrant *in desert scrub habitat.* (Mountain "islands" have breeding populations of Broad-tailed and Blue-throated Hummingbirds (*Selasphorus platycercus, Lampornis clemenciae*).) In Big Bend National Park, Texas, in the northern third of the Chihuahuan Desert, Lucifer Hummingbird (*Calothorax lucifer)* is at the northern edge of its range and is resident from March to September (Wauer 1973, Kuban 1977, Scott 1983). It is rare on the outwash plains, the habitat favored by Costa's Hummingbird in the Sonoran Desert. Instead, it nests on arid slopes in mountain foothills and canyons at the upper elevational end of ocotillo's habitat. *Archilochus alexandri* is near the southern end of its range in Big Bend, and like *C. lucifer* is rare in desert scrub habitat. *Archilochus alexandri* nests in the foothills in wooded canyons, occasionally on arid slopes, in isolated oases of cottonwoods (*Populus* sp.) on the outwash plains, and in riparian vegetation along the Rio Grande. Although it might be expected that *A. alexandri* migrating to breeding grounds in the central-western United States would pass through the Chihuahuan Desert in large numbers, I have seen no conspicuous passages. The status of hummingbirds in the Mexican portion of the Chihuahuan Desert is poorly known. *Calothorax lucifer* is the species likely to enter ocotillo habitat, but most Mexican records of *C. lucifer* are from middle elevation sites above desert scrub (Scott, unpublished data).

The scarcity of hummingbirds (residents or migrants) in spring in Chihuahuan desert scrub seems due to a shortage of nectar sources, which in turn may be due to the Chihuahuan climate. This interior desert is higher in elevation than the Sonoran, has a longer cold season, and receives less winter rainfall from Pacific fronts (Turner and Brown 1982; Schmidt 1986). Seventy to 80% of annual rainfall occurs between May and October (Schmidt 1986). Perhaps because of the rainfall pattern, few nectar sources suitable for hummingbirds, other than ocotillo, bloom on the outwash plains in spring. Examples include *Castilleja latebracteata,* an uncommon species parasitic on

Agave lechuguilla , and *Penstemon havardii*, a Big Bend endemic restricted to several canyons and washes. None of these is nearly as widespread or productive of nectar as *Justicia californica* in the western Sonoran Desert. Furthermore, the flowering period of *F. splendens* in the Chihuahuan Desert is shorter (3-4 weeks) than in the Sonoran Desert, and exploitation of ocotillo nectar by carpenter bees means that little is available to hummingbirds in some years.

Henrickson (1972), who collected *F. splendens* throughout its range, drew attention to the rarity of hummingbirds at Chihuahuan Desert sites and to the prevalence of carpenter bees. He noted that the exserted stamens and rolled-back corolla lobes of *F. splendens* give the large bees a platform on which to rest while piercing the base of the flower tube for nectar. In the process the bee's abdomen contacts anthers and is likely to contact one or more of three stigmas situated among or slightly below the anthers. Females gathering pollen brush their abdomen or legs over the anthers, often while piercing for nectar (Henrickson 1972, Waser 1979, Scott, pers. obs.). Thus, although carpenter bees obtain nectar from *F. splendens* by "nectar-robbing," they contact sexual parts of the flower, even when not deliberately gathering pollen. At other desert flowers adapted for hummingbirds (*Penstemon havardii, Anisacanthus linearis*) or bumblebees (*Chilopsis linearis, Tecoma stans*), carpenter bees obtain nectar by the same method and do not contact sexual parts because these are contained within the floral tube or extend far beyond it (*A. linearis*). Carpenter bees probably contact the anthers and stigmas of *F. splendens* more frequently than do hummingbirds, which (in Texas) insert only part of the bill into the relatively short tube. At least one other flower pollinated by *X. c. arizonensis, Agave toumeyana* (range: south-central Arizona), has a morphology similar to *F. splendens*. The bee rests on exserted anthers while probing the base of the floral tube (Schaffer and Schaffer 1977).

Xylocopa californica arizonensis occurs throughout the range of *F. splendens* but is "widely discontinuous" (Hurd 1955: map 1, Hurd and Linsley 1975: Fig. 18,

Henrickson 1972: Fig. 23). Presence of carpenter bees depends on availability of nesting substrates. Over most of its range *X. c. arizonensis* uses the dead, softwood flower stalks of various species of *Agave, Dasylirion,* and *Yucca* (Hurd 1955, Krombein et al. 1979). In southern California, however, the species nests in fronds of the palm *Washingtonia filifera* (O'Brien and O'Brien 1966) and does not use the apparently suitable stalks of *Agave deserti*, which are common on the outwash plains among stands of ocotillo.

Waser's study of Fouquieria splendens *at Tucson*

Waser (1979) studied the temporal pattern of pollinator availability and its importance in selecting for timing of flowering in *F. splendens*. He measured seasonal and annual fluctuations in abundance of hummingbirds and carpenter bees at Tucson, Arizona, in the eastern Sonoran Desert. Seasonal availability of hummingbirds was predictable: most were northward-migrating Black-chinned Hummingbirds, whose numbers peaked at approximately the same time each year. However, their abundance varied as much as seven-fold between years. Abundance of carpenter bees varied to an even greater extent. The regression of seed set on pollinator abundance (positive with a fairly steep slope) suggested that seed set was often limited by availability of pollinators.

Waser hypothesized that the timing and duration of flowering was an adaptation to a brief, predictable period of migrant hummingbird abundance. The hypothesis was supported by two sets of data. Exclusion experiments (using chicken wire cages) showed that carpenter bees were effective pollinators, but that seed set was 10-30% greater when flowers were accessible to hummingbirds as well as to bees. The complementary experiment (exposing flowers to hummingbirds only, excluding bees) was not feasible. Waser also found that natural seed set was highest when the peak of flowering was closest to the midpoint of hummingbird migration.

I evaluate the validity of Waser's hypothesis for California and Texas populations of *F. splendens*, where availability of pollinators and flowering behavior differ to varying degrees from conditions in Tucson. I hypothesize that in Texas the brief period of massive flowering in spring reflects selection for the ability to attract breeding carpenter bees.

Chapter 2

Pollination ecology of Ocotillo in the northern Chihuahuan Desert

At Big Bend National Park (BBNP), Texas, I made a three-year study of the pollination ecology of *Fouquieria splendens* and the importance of its floral rewards to carpenter bees and to hummingbirds. The apparent lack of a widespread hummingbird species, resident or migrant, in Chihuahuan Desert scrub, and Henrickson's (1972) observations on the prevalence of carpenter bees in Texas and Coahuila suggested that hummingbirds would not be generally common or reliable visitors. However, hummingbirds are locally common in one of the two distinctive habitats occupied by ocotillo in BBNP (mountain foothills). One set of objectives was: (1) to determine whether there was important local variation in the identity of ocotillo's primary pollinator; (2) to compare local geographic variation with yearly fluctuations in visitation intensity; and (3) to determine whether hummingbirds and carpenter bees competed for nectar in the habitat where hummingbirds were common. Other goals were (1) to determine the predictability of *Fouquieria splendens* as a floral resource; (2) to characterize its breeding system; and (3) to identify characteristics of pollinators and floral traits that contribute to pollination success.

Big Bend National Park (BBNP) protects 1760 km^2 in Brewster County, Texas, USA, in the northern Chihuahuan Desert (Fig. 2.1). In its center are the igneous Chisos Mountains (29°15'N, 103°15'W; highest elevation 2374 m). Outwash plains (bajadas) fan out from the mountain foothills at 1090-1270 m and descend to the Rio Grande and local tributaries. The outwash plains vegetation is desert scrub, described in Henrickson and Johnston (1986). It includes creosotebush (*Larrea tridentata*), ocotillo, lechuguilla (*Agave lechuguilla*), Torrey yucca (*Yucca torreyi*), prickly pear (*Opuntia* spp.), and chino grama grass (*Bouteloua ramosa*). Honey mesquite (*Prosopis*

glandulosa), desert-willow (*Chilopsis linearis*), and acacias (*Acacia* spp.) are common in the usually dry watercourses. The mountain foothills support a sotol-grassland (Wauer 1971) in which sotol (*Dasylirion leiophyllum*), century plant (*Agave havardiana*), ocotillo, and chino grama are prominent. Annual rainfall at an upper bajada site, Panther Junction (1136 m), is 349 ± 107 mm ($\bar{x}$ ± S.D., n = 31, 1956-1986; National Park Service data, statistics courtesy of A. E. Dunham). BBNP has the dry winter-spring, wet summer-fall seasons characteristic of the Chihuahuan Desert (Schmidt 1986). Monthly rainfall averages 8-15 mm from November to April and 40-55 mm from May to October (see Table 2.1).

Fouquieria splendens is common from the lowest elevations along the Rio Grande (650 m) to approximately 1600 m in the Chisos Mountains. Although abundant on rocky slopes in the foothills, ocotillo has a more extensive distribution on the outwash plains. Previous study of the nesting ecology of Lucifer and Black-chinned hummingbirds (*Calothorax lucifer, Archilochus alexandri*) had shown that both are rare in spring on the outwash plains, but are locally common in the foothills habitat, where Lucifer Hummingbirds nest on arid slopes among ocotillos and Black-chinned nest in wooded canyons (Scott 1983). I expected that their visitation rates to ocotillo would be greatest in the foothills, and that they would be important pollinators of ocotillo there.

With respect to carpenter bees, Waser (1979) pointed out that proximity to nest plants would influence their visitation frequency. Species of three plant genera used by *X. c. arizonensis, Agave, Dasylirion*, and *Yucca* (Hurd 1955), are common in both the mountains and outwash plains of BBNP, so I anticipated that most ocotillo populations would be close to nesting carpenter bees. In summary, I expected that carpenter bees would be the primary pollinator of *F. splendens* on the outwash plains, and that both bees and hummingbirds would pollinate foothills plants, with the relative importance of each depending on local abundances and effects of interspecific competition for nectar.

In Waser's (1979) experiments, mechanical exclusion of hummingbirds caused a significant reduction in seed set. It was unclear whether the reduction was due to inefficient transfer of pollen by carpenter bees or simply to low visitation rates. Other studies of flowers visited by both hummingbirds and bees suggest that bees, when abundant, can greatly reduce hummingbird visit rates, usually by their impact on the nectar supply (Brown et al. 1981, Roubik 1982). It is also possible that competition from bees would cause hummingbirds to increase their visit rate, if the lower nectar levels were still sufficient to balance energy expenditures and if flowers were abundant (McDade and Kinsman 1980). Therefore I was especially interested in observing visit rates and nectar levels at sites where both carpenter bees and hummingbirds were common.

METHODS

Selection of study sites and assessment of pollinator availability

To compare pollinator activity in the two habitats, I selected ocotillo stands at three sites in the foothills of the Chisos Mountains and at three sites on the outwash plains, and quantified visitation rates (see below). "Stands" were fairly dense aggregations of plants, conspicuous from a distance, containing plants 2-3 m tall. The sites are mapped in Figure 2.1 and described in Tables 2.2 and 2.3. Each foothills site was in an area where Lucifer and Black-chinned hummingbirds either nested in high density or at least were seen regularly. I estimated the density of nesting hummingbirds at Panther Canyon in 1985, prior to initiation of the ocotillo study. At Rough Spring, I searched for nests within 1 km of the site on an irregular schedule in 1986 and 1987. At other sites, estimates of hummingbird abundance were based on visitation rates and additional casual observations. At all sites I examined dead flower stalks of *Dasylirion leiophyllum*, *Agave* spp., and *Yucca elata* for carpenter bee nests.

On the outwash plains, observations were made at the same plots each year (1986-1988). In the foothills, no observations were made in 1987 because a freeze in late March killed budding inflorescences. In 1988, substitutions were made for two foothills sites (Panther, Basin) observed in 1986, which were 2.5 km and 1 km, respectively, from residential areas that provided sugar-water feeders for hummingbirds. Availability of feeders increases local density of hummingbirds and might affect visitation rates to natural nectar sources in various ways. Other plots were at least 5 km from hummingbird feeders (Tables 2.2, 2.3).

Phenology and flower production

At each site 20 ocotillo plants were permanently marked in April 1986. The flowering status of each inflorescence on these plants was recorded at approximately weekly intervals. An inflorescence was assigned to one of three categories: all flowers in bud, at least one mature flower, flowering finished (or fruits developing). I assumed that an inflorescence began flowering at the midpoint between dates on which it was "in bud" and "in flower". By such methods the duration of flowering for inflorescences and whole plants was estimated with a probable margin of error of 3-4 days.

The number of flowers per inflorescence varied from 10 to over 200, so that inflorescence number was only a rough index of a plant's flower output. In 1987 and 1988, during the middle of flowering, I counted the total number of flowers produced (buds + mature flowers + finished flowers) by ten marked plants at three sites.

Breeding system

I tested the breeding system of *F. splendens* in 1987 at Maverick. I applied five treatments (Table 2.5), each to the flowers of a single inflorescence, and replicated treatments on six plants. In four treatments inflorescences were bagged with a fine mesh netting, which was removed during hand-pollinations. Flowers that opened

between 7 and 14 April were treated; any flowers that had opened prior to 7 April were cut, and on 14 April remaining buds were cut. I checked developing fruits weekly and collected them one month after treatments ended, just before capsules opened. I placed individual fruits in separate envelopes and later counted seeds. In the *autogamy* treatment, the inflorescence remained bagged throughout the week. In three hand-pollination treatments I picked a donor flower and brushed its anthers against the stigmas of recipient flowers. Each flower was treated once daily. Flowers opened at various times and remained open for about 1.5 days, so a given flower was treated one or two times. In the *hand-self* treatment, the donor flower came from another inflorescence on the same plant. In *hand-outcross* treatments I applied pollen from the nearest ocotillo or from plants 1 km distant. In the *natural* treatment, an inflorescence was marked but not bagged and hence was accessible to any pollinator. I analyzed effects on fruit set and seed set separately. Values of fruit set (the proportion of treated flowers forming fruits) were arc-sine-transformed, then analyzed by two-way ANOVA, with plants as blocks. Four *a priori* contrasts of treatment effects were tested using the method of least significant difference (Steel and Torrie 1980). In the analysis of effects on seed set, multiple values for each plant-treatment combination allowed for a test of plant x treatment interactions.

Visitation rates and standing crops

I observed visitation to flowers twice each season at each site. Observation periods were at least five days apart, began within an hour after sunrise, and lasted three hours (1986) or two hours (1987-1988). I selected a patch of plants in full flower, typically four to six plants with 80-150 inflorescences in flower. Patches were large enough to increase the likelihood of seeing hummingbird visits when the rate of visitation was low, and small enough to permit one observer to detect all visits and quantify the rate as visits per inflorescence per hour. To avoid disturbing the birds or

influencing their rate of approach, I sat 5-10 m from the nearest plant. It was not feasible to quantify carpenter bee visitation in these large patches in the same way, because several carpenter bees were sometimes active simultaneously. At 10-minute intervals, I scanned all inflorescences in the patch with binoculars for one minute (Boinski and Scott 1986) and counted carpenter bees visiting flowers. An alternative measure of carpenter bee abundance was derived from examination of flowers after the observation period (see below). During scans I also counted bumblebees and other large insects. When honeybees and smaller solitary bees were common, I walked through the patch at 20-minute intervals, examined inflorescences, and counted the number taking nectar or pollen.

Following each observation period (less frequently in 1986), I sampled flowers to record signs of visitation (cuts, rips, and punctures of corollas) and to measure the standing crop of nectar and pollen. Sampling occurred between 10:00 am and 2:00 pm Central Daylight Time. I collected five flowers from one inflorescence per plant on a total of six to ten plants (n= 30 or 50 flowers). Signs of visitation were identified as follows. Carpenter bees made short (3 mm long) cuts on the corolla at its juncture with the calyx. The *mean number of carpenter bee cuts per flower* was considered the best index of carpenter bee visitation rate. Scott's Orioles (*Icterus parisorum*) ripped corollas when probing them with their relatively large bills. Rips typically extended from the distal end of the tube to its junction with the calyx. Verdins (*Auriparus flaviceps*) robbed nectar by puncturing the base of corolla tube with their small pointed bills, leaving a triangular puncture. Queen bumblebees (*Bombus sonorus*) pushed their heads into the corolla tube while attempting to reach nectar, and sometimes split the tube in the same manner as orioles.

Nectar was extracted with a 10-microliter micropipet, the volume measured, and its concentration (mass of solutes/mass of solution) determined with a hand refractometer (Reichert Scientific Instruments Model 10431). Volumes from two or

more flowers were combined when necessary to obtain a concentration reading. Samples exceeding a concentration of 50% were diluted with water, and the true concentration was calculated later. I sent nectar samples dried on filter paper to C. Edward Freeman (University of Texas at El Paso), who analyzed sugar composition. I assumed that all solutes were sugar molecules, and calculated sugar quantities as milligrams of sucrose-equivalent sugars, following Bolten et al. (1979). I estimated availability of pollen by assigning each flower a score of 0, 1, 2, 3 or 4 based on a naked-eye inspection of anthers, where 0 = no pollen (or very little) remaining on anthers, and 4 = anthers bearing a full load of pollen.

Carpenter bee data were analyzed statistically using a nested analysis of variance with four levels of variation: among years; among habitats within years; among sites within habitats and years; among dates within sites, habitats, and years. Variation in pollinator activity among habitats and among years was of primary interest. I estimated the percentage of total variance accounted for by each level. The data were unbalanced because sample sizes of flowers varied, as did the number of sites; therefore, tests of significance were not carried out (Sokal and Rohlf 1981). Hummingbird visitation data did not meet the assumptions of analysis of variance because of many zero values. The effects of habitat and year on hummingbird visits were analyzed with the non-parametric Mann-Whitney U-Test.

Pollination success

For each site and year I estimated mean seed set (seeds/fruit). A month after flowering ended I collected samples of 20-40 fruits from inflorescences marked early in the flowering period (2-4 inflorescences/plant, 5 plants/site). I collected adjacent fruits without regard to size. In 1987 (a year of low fruit set), I collected all fruits on marked inflorescences. To determine the upper limit for seed set, I collected 25 flowers (5 flowers/plant) at two sites in 1988 and counted ovules using a dissecting

microscope. I correlated seed set at each site with the mean number of carpenter bee cuts per flower, based on one or two samples of 30-50 flowers (Table 2.3). Fruit samples were collected from permanently marked plants; flower samples (usually two per flowering period) were taken from adjacent unmarked plants.

I measured fruit set in 1987 and 1988 at outwash plains sites. During flowering I counted buds and flowers on marked inflorescences; near the end of the month of fruit maturation I counted fruits. In 1987 fruit set was determined for two inflorescences/plant. In 1988 I determined fruit set for entire plants (10/site), marking each inflorescence and counting all flowers and fruits produced.

I tested for resource limitation of fruit set and seed set at Maverick in 1987 (see Breeding Test) and 1988. On 6 April 1988 I hand-pollinated flowers on six inflorescences (2/plant), applied to each flower pollen from two neighboring plants instead of one, and marked flowers on six control inflorescences. Both groups of flowers were accessible to pollinators.

Foraging behavior

In 1988 I observed single ocotillo plants for 2-hour periods, during which I recorded the number of flowers visited by each carpenter bee or other visitor. Observations were made at four sites on a total of six dates. I collected 30 flowers (5/inflorescence) before and after the observation period and measured nectar and pollen levels. To investigate whether bees respond to higher than average floral rewards by visiting more flowers, I bagged all inflorescences on one plant for 24 hours and unbagged them in mid-afternoon. At one site I followed individual female carpenter bees during portions of foraging bouts. Selecting a bee that was already foraging, I began observations when it moved to a new plant and followed it until she left the patch or I lost sight of it. I recorded the number of flowers and inflorescences visited on each plant, whether flowers were pierced for nectar, and accumulation of pollen on the bee.

Floral traits

I estimated the daily nectar production of an average flower in two ways. I used data from the standing crop samples made on dates when visitation by carpenter bees and other nectar consumers was low. The standing crop in *uncut*, mature flowers of unknown age was taken to represent approximately one day's production. I also bagged heavily visited inflorescences with a fine netting and compared the standing crop at the time of bagging with the amount accumulated after 12, 18, and 24 hours (Waser 1978) in flowers cut by bees prior to bagging, and therefore were known to have been open throughout the interval. When sampling nectar, I measured corolla tube length and diameter, and exsertion of anthers and stigmas beyond the mouth of the corolla tube. The corolla tube was measured with the calyx attached: I placed one caliper point at the base of the calyx and the other at the well-defined mouth of the tube, where the lobes roll backward. I measured five flowers from one inflorescence per plant, and usually 30 flowers per sampling date.

I investigated timing of flower opening by marking one or two inflorescences on several plants, cutting all open flowers, and counting the number that subsequently opened at intervals of 3-6 hours during the day.

RESULTS

Local abundances of hummingbirds and carpenter bees

At two foothills sites, the density of nesting hummingbirds, especially *Calothorax lucifer*, was high; nesting occurred from April to August (Tables 2.2, 2.4). *Calothorax lucifer* commonly nested on branches of *F. splendens* in summer, when the branches were green with leaves. In spring, during flowering of ocotillo, nests were usually built on cane cholla (*Opuntia imbricata*) or dead flower stalks of *Agave lechuguilla*. At other foothills sites, hummingbird density was low and no nests were found; but birds were

regularly seen during flowering of ocotillo and a few probably nested within 1-2 km. Only one hummingbird nest was found near an outwash plains site (Table 2.3). Typically, hummingbirds occurred as occasional transients at such sites.

Carpenter bee nests were found within 1 km of all five foothills sites and at one outwash plains site (Tables 2.2, 2.3). Another outwash plains site was within foraging distance (2-3 km) of carpenter bee nests, but a third was remote (> 5 km) from suitable nest plants.

Ocotillo phenology

All ocotillo populations flowered once annually, beginning sometime between 25 March and 15 April, except for foothills sites in 1987. A freeze on 30 March 1987 (-4^{o} C at Panther Junction, 1136 m) killed almost all budding inflorescences at sites above 1100 m. The onset of flowering varied by as much as 20 days between years at a site (Figures 2.2 a-c), reflecting variation in March temperatures, which were approximately 4^{o} C cooler in 1987 than in 1986 (Figure 2.3). Within any year, flowering began 5 to 8 days earlier at Maverick (860 m) than at KBar (1000 m). The median duration of flowering at outwash plains sites (20 plants/site, Figures 2.2 a-c) was 38.5 days (range: 27 - 48 days, n = 9), but the peak flowering period was much shorter: 90% of all inflorescences at a site completed flowering in a period of 22 days (median; range: 20 - 29 days). The 90% completion interval did not vary significantly among years (χ^2_r = 1.13, df = 2, p > 0.5; Friedman ANOVA by ranks, blocking on sites). Thus the duration of flowering episodes was consistent and relatively brief. This was due to impressive synchrony among plants that varied several-fold in flower crop size. The average number of flowers opened per day increased significantly with crop size ($P < 0.001$ for each site and year) (Figure 2.4 a-c). An average plant, with 1930 flowers, opened 71 flowers per day. Fruits began dehiscing 25-30 days after flowering ended, with the result that seeds were dispersed (by gravity or wind) 1-2 weeks before the

onset of summer rains in 1986 and 1988. In 1987, rains of > 25 mm occurred during flowering and again during fruit dehiscence.

Flower and nectar production

Although dry season rainfall varied substantially among years (Table 2.1), ocotillo was remarkably consistent in flower production. Plants produced large numbers of inflorescences in all three years at outwash plains sites. There was significant but relatively minor annual variation in inflorescence production at each site (Fig. 2.5; Maverick: $F_{2,38} = 7.2$, $P < 0.01$; Dugout: $F_{2,38} = 5.0$, $P < 0.05$; KBar: $F_{2,38} = 5.8$, $P < 0.01$). Flower production, measured in 1987 and 1988, did not vary significantly at Maverick ($t_9 = 1.73$, $P > 0.10$) or Dugout ($t_9 = 1.77$, $P > 0.10$), but did at KBar ($t_9 = 4.16$, $P < 0.01$), where the difference was approximately two-fold (Figure 2.6).

An average flower accumulated 1.1 to 4.6 mg nectar sugar when carpenter bees and other nectar consumers were rare (Table 2.5). Nectar concentration was higher in the hot, dry spring of 1988 than in 1987 (Figure 2.3). Sugar composition averaged 73.3% sucrose, 13.5% glucose, and 13.1% fructose (n = 5, C. E. Freeman, in litt.; see also Freeman et al. 1984). Flowers cut by carpenter bees continued to produce nectar: approximately 3.1 mg in 24 hours, including some nocturnal production (Figure 2.7). Production was highest in the afternoon (approximately 0.2 mg sugar/hour).

Breeding system

The Maverick population was largely self-incompatible (Table 2.6). With respect to fruit set, plants did not show significant individual variation in their responses to pollination treatments (Table 2.7). With respect to seed set, there was significant variation among plants (Table 2.8), but each plant had higher seed set in outcrossing treatments than in selfing treatments (contrast 2). Flowers that received

only self pollen had 10% fruit set, far less than outcrossed flowers (Table 2.7, contrast 2); most fruits contained only one or two seeds. Overall fecundity (seeds/flower) was 4% of that of hand-outcrossed flowers. Autogamy and geitonogamy (self-pollination by hand) treatments did not differ (contrast 1). Fruit set was high in both hand-outcross treatments, and significantly greater in the near-neighbor treatment (Table 2.7, contrast 3). Seed set in outcrossing treatments (4.3, 4.0 seeds/fruit) was low relative to mean ovule number (12.6 ovules/flower; see below) and also relative to natural seed set in the previous year (9.6 seeds/fruit, Table 2.12).

Flowers open to pollinator visits had lower fruit set (Table 2.7, contrast 4) than flowers outcrossed by hand. Inadequate pollinator service limited overall fecundity to 57% of that of hand-outcrossed flowers (near neighbour treatment); but this was not as severe a reduction as I expected. No carpenter bees or other visitors were seen in a 2-hour observation period during the week of treatment (Table 2.9: Maverick 1987, day 1), nor on daily visits to the patch, and unbagged flowers contained high levels of nectar and pollen (Table 2.9). The local agent of pollen transfer during this week was not identified. In the following year, a supplemental pollination test revealed a much greater deficiency in pollinator service at this site (see below).

Visitation rates and impact on floral rewards

In 1986 and 1988, carpenter bees were by far the most frequent visitor to ocotillo flowers (Tables 2.9, 2.10). Cuts on flowers, which indicate the minimum number of visits, showed that an average flower received 3-5 visits in 1986 and 1-4 visits in 1988, except at one site (Maverick) in the latter year. In these two years, hummingbirds rarely appeared at desert sites. In the foothills, they visited ocotillo rarely or not at all on six of 12 dates, although birds were always present at these sites. On four dates in 1988 and once in 1986, hummingbirds made at least 0.09

visits/inflorescence x hour. At such a rate an average flower would be visited approximately once during 18 daylight hours of flower life, assuming that a bird visited half of the open flowers on an inflorescence. The highest rate of visitation by hummingbirds (0.24 visits/inflorescence x hour, Cattail 1988) implies a total of 2.2 visits to an average flower. Only at this site did hummingbirds visit at a rate roughly equivalent to that of carpenter bees.

Other nectar consumers were even less frequent visitors (Table 2.10). Queen bumblebees *(Bombus sonorus)* appeared during roughly half of the observation periods, but were common only twice. Feral honeybees *(Apis mellifera)* took nectar only from the open bases of old, detaching corollas. Pollen-gathering bees, other than carpenter bees, were rare or absent in 1986 and 1988.

The intensive visitation by carpenter bees in 1986 and 1988 was reflected in midday availability of nectar and pollen (Table 2.9). Flower visits by either sex almost always involved piercing the corolla to seek nectar. Many females also gathered pollen simultaneously; they rubbed their abdomen over anthers and packed pollen in the scopal hairs of their hind legs. On average, with the lone exception of the Maverick site in 1988, flowers contained < 0.2 ul nectar or < 0.2 mg nectar-sugar. The standing crop was as low on dates when hummingbirds did not visit as on the few dates when they visited flowers. Frequently (four of five dates in 1986, eight of 12 dates in 1988) more than 50% of flowers in midday samples were stripped of pollen.

In 1987 carpenter bees were much less common. Although large quantities of nectar accumulated at desert sites (Table 2.9), rates of visitation by other nectar consumers did not increase, except on one date when a beefly (*Anthrax xylocopae*) visited commonly. No hummingbirds were observed in 1987. However, surplus pollen was harvested by two small halictid bee species, especially during the latter half of the flowering period. One or both species were abundant on four of six dates (Table 2.10).

Effects of habitat and year on carpenter bee visitation

Variation among years accounted for 52.5% of the total variance in carpenter bee cuts/flower (Table 2.11). Habitat accounted for none of the variance (the variance component was negative.) Variation among sites within habitats, and among dates within sites was minor. There was substantial variation among flowers within samples (error), probably because samples included flowers of different ages, which had been exposed to carpenter bees for different numbers of hours. Thus within any year there was little geographic variation in the availability of carpenter bees to ocotillo populations. This was probably due to two factors: broad distribution of three acceptable nest plant species, and large foraging ranges.

Carpenter bees nested in both foothills and outwash plains habitats. I found nests near all sites except Maverick (Tables 2.2, 2.3), and at elevations as low as 650 m along the Rio Grande (see Chapter 3). Nesting density was probably greatest in the foothills. All four nest plant species are common in that habitat, the largest *Agave* species (*A. havardiana)* is restricted to it, and bees seem to prefer nest locations on slopes rather than on flat terrain. Despite local variation in nesting density, visitation rates to ocotillo were relatively even over broad areas, probably because bees searched for under-exploited patches. Carpenter bees are strong fliers. At outwash plains sites (Dugout, KBar) I observed pollen-laden females conclude foraging bouts, rise high above ocotillos, and then fly straight toward foothills slopes several km distant. I sometimes could track their flight for several hundred meters with binoculars.

One of the outwash plains sites, however, was remote from nesting aggregations. Within approximately 5 km of Maverick, even the nearly ubiquitous *Agave lechuguilla* was scarce. Carpenter bees "discovered" the Maverick patch much later than other sites in 1987 and 1988 (Table 2.9). In the latter year, they appeared only in the last days of flowering (after the second observation period listed in Table 2.9). Results at Maverick

show the importance of proximity (on a scale of several km) to carpenter bee nest plants.

The marked variation between years in visitation rates to ocotillo probably reflected changes in carpenter bee population density rather than preference for an alternative flower type (see Chapter 3). I recorded casual observations of use of other flowers by carpenter bees and saw them rarely at other species in 1987 (Table 3.1). Although ocotillo floral rewards are their major spring breeding resource, the bees have a long, intermittently active season and other factors affect population density (Chapter 3).

Effects of habitat, year, and carpenter bees on hummingbird visitation

As expected from the distribution of their nests, hummingbirds visited ocotillos more frequently at foothills sites than on the outwash plains (Mann-Whitney U-Test: $U = 111$, $n_1 = n_2 = 12$, $P < 0.025$, 1-tailed; 1986 and 1988 data), but even in the foothills visitation was generally low. There was no evidence of a wave of migrant hummingbirds in either habitat. Visitation rates in the foothills were not significantly different in 1986 and 1988 ($U = 25$, $n_1 = n_2 = 6$, $P > 0.05$, 2-tailed); however, relatively high visit rates were recorded in 1988 at Cattail, where a male Black-chinned defended an ocotillo patch temporarily against a male Lucifer.

Spring in 1988 was unusually dry (Table 2.1) and alternative nectar sources were scarce. *Penstemon havardii*, normally available in the foothills during flowering of ocotillo, failed to flower. It is doubtful that ocotillo flowers were a profitable energy source for hummingbirds in 1988, except for brief periods. Frequent visits by bees and sometimes hummingbirds kept the standing crop of ocotillo nectar sugar very low (< 0.2 mg/flower) at most sites. Hummingbirds did not appear at Maverick (where rewards were high); presumably, Maverick was beyond the foraging range of the nearest breeding birds.

In contrast, 1987 was a relatively cool, wet spring; nectar was superabundant and carpenter bee density was low. Because of the scarcity of bees, foothills populations of ocotillo would have been rewarding to hummingbirds, but ocotillos at elevations above 1100 m failed to flower because of a late freeze (possibly a source of carpenter bee mortality). *Penstemon havardii* and *Castilleja lanata* flowered after the freeze; their nectar was superabundant (standing crops exceeded 2 mg sugar/flower) near hummingbird nesting grounds, and birds fed at these flowers while ocotillo flowered at more distant sites on the outwash plains.

Aggressive interactions between carpenter bees and hummingbirds were rare and brief. The low visit rates by hummingbirds at foothills sites in 1986 and 1988 appeared to be due to the very low nectar rewards typically present in ocotillo flowers (Table 2.9), a consequence of dawn-to-dusk harvesting by carpenter bees.

Pollination success

The number of ovules in ovaries of ocotillo flowers was variable. All flowers examined at Maverick and the Basin had 3 locules/ovary and 3-7 ovules/locule. Flowers at Maverick contained 12.6 $\pm$ 2.2 ovules ($\bar{x} \pm$ S.D., n = 25) while those from the Basin contained 14.0 $\pm$ 2.6 ovules. Based on these data, I assumed that the maximum possible mean seed set at other sites was 13.3 seeds/fruit.

Seed set varied in parallel with carpenter bee visitation (Tables 2.9, 2.12). It was highest in 1986, dropped sharply in 1987, rose in 1988 to values approaching those of 1986, and varied little among sites within a year (with the exception of Maverick 1988). Regression of seed set on the mean number of carpenter bee cuts per flower explained 89% of the variance in mean seed set values (Figure 2.8). The regression equation suggests that: (1) on average, each carpenter bee visit resulted in production of 1.6 additional seeds, up to an asymptote of approximately 10 seeds; (2) seed set was limited by inadequate pollinator service when carpenter bee visitation was

low ($\leq$ 1.0 cuts/flower); and (3) intensive cutting of corollas (> 3.5 cuts/flower) had no adverse effect on seed set.

The abundance of most other potential pollinators did not covary with carpenter bees (Tables 2.9, 2.10). Queen bumblebees were an exception; like carpenter bees, they were relatively common in 1986 and 1988 and rare in 1987, but only twice were they common enough to have visited all flowers even once. The virtual absence of hummingbirds at outwash plains sites cannot explain changes in seed set there. At the one foothills site (Cattail 1988) where hummingbirds visited frequently enough to have had an effect (if they contacted anthers and stigmas regularly), seed set did not differ significantly from two other sites (Rough Spring and Pummel, Table 2.12) where hummingbird visitation was lower and carpenter bees were slightly more common. Small pollen-gathering halictid bees were common only in 1987 (Table 2.10), when the scarcity of carpenter bees left a bonanza of ocotillo pollen for other visitors. These bees reduced available pollen to low levels on four dates (Table 2.9), comparable to the effects of carpenter bees in 1986 and 1988. Yet seed set and fruit set were low (Table 2.12), and the limited pollination success may have been due mainly to carpenter bees. The full pollen load of a single flower was more than one halictid could carry, and casual observations suggested that individuals moved infrequently between plants during a foraging bout. They were probably poor vectors of outcross pollen.

The most striking instance of pollinator limitation of fruit set and seed set occurred at Maverick in 1988. It was obvious that flowers there were not being visited; they held large volumes of nectar throughout the day and full loads of pollen (Table 2.9). Seed set of hand-outcrossed flowers there was 27 times greater than controls accessible to pollinators (Table 2.13).

Big Bend ocotillos experienced very high levels of pollination success when carpenter bees visited frequently. Mean seed set per fruit when flowers had > 2 cuts was 54% to 77% of the maximum possible. Average fruit set on whole plants exceeded 80%

at two sites in 1988 (Table 2.12). At Dugout, plants produced 1,668 ± 968 fruits ($\bar{x}$ ± S.D., n = 10) and an estimated 13,844 seeds/plant; at K-Bar, 1,316 ± 932 fruits, and 11,318 seeds/plant. Clearly ocotillo is capable of maturing a high proportion of its massive annual output of flowers and ovules into fruits and seeds. Dependence on a high density of pollinators was underscored by the poor reproductive output at Maverick in 1988 (Table 2.12), where plants produced 495 ± 217 fruits and 991 seeds/plant. The limited fruit set and seed set that occurred was due to discovery of the site by carpenter bees in the last few days of flowering.

At Dugout and KBar in 1988, the slope of the linear regression of percent fruit set on number of flowers (Figure 2.9) was not significantly different from zero (Dugout: $F_{1,8} = 0.07$, $P = 0.80$; KBar: $F_{1,8} = 1.74$, $P = 0.22$). Thus pollination success was not adversely affected by opening large numbers of flowers per day, and total fruit set increased with flower output.

Foraging behavior of carpenter bees

Only carpenter bees and queen bumblebees visited flowers at single ocotillo plants watched in 1988 (Table 2.14). At one plant, bumblebees visited more flowers, but they were absent or rare at four other plants. Plants were visited 8-15 times per hour by carpenter bees. Female bees, usually more numerous than males, visited a surprisingly small percentage of the open flowers on any plant (typically 4-8%), although there was much variation (Table 2.14; Figure 2.10). Nectar crops were low at the beginning of observation periods and were reduced 30-80% after two hours. Pollen availability was also low initially and declined.

After 24 hours of bagging, flowers on an experimental plant at KBar had relatively high initial rewards of nectar and pollen (Table 2.14: 27 April). The number of bees visiting the plant per hour was similar to values for plants with low standing crops on other dates, but bees visited significantly more flowers on the experimental

plant ($t' = 2.34$, effective df = 23.5, $P < 0.05$, two-tailed; variances for the experimental plant and for all others combined were unequal; Steel and Torrie 1980). Four returned to the experimental plant for a second visit after visiting fewer than five flowers on an adjacent plant.

Individual female bees visited many plants (5-29) and flowers (83-247) during the parts of foraging bouts observed (Table 2.15), but again relatively few flowers per plant (Figure 2.10). They harvested nectar and pollen rather quickly, visiting one flower for every 4-8 seconds of foraging time, which included much time hovering around inflorescences before landing. On almost all visits, they pierced the corolla base (or perhaps probed other cuts) to obtain nectar, and their abdomens made strong contact with the exserted anthers; presumably, stigmas were contacted frequently. In several cases pollen accumulated noticeably on the bee's abdomen and legs during the bout.

Timing of flower opening and corolla tube length

Flowers opened at various times of day and overnight (Table 2.16), resulting in staggered presentation of pollen, an important reward for nest-provisioning female bees. A majority of flowers (ca. 60%) opened between 11:00 A.M. and 6:00 P.M.

The mean length of the corolla tube, pooling data from eight sites (Table 2.17), was 14.1 $\pm$ 1.6 mm ($\pm$ S.D., n = 517). This was long enough to make the nectar difficult for bumblebee queens to reach and inaccessible to most other bees, including feral honeybees. The tubes were approximately 6 mm shorter than those of California flowers (Table 2.17).

DISCUSSION

Several lines of evidence support the conclusions that carpenter bees were the primary pollinator of *F. splendens* in both habitats and were highly effective when they

harvested most floral rewards. These include the increasing slope of the regression of seed set on number of carpenter bee cuts and the rarity of other potential pollinators. When the average flower received at least two carpenter bee visits, natural fruit set was as high and seed set was higher than when flowers were outcrossed by hand. My results confirm and extend Waser's (1979) finding (see Chapter 1). When abundant, carpenter bees were not merely competent but excellent pollinators of *F. splendens.*

Nectar characteristics of *F. splendens* are suitable for hummingbirds. Production of 1 to 4 mg sugar/flower/day is typical of hummingbird flowers of the western United States (e.g., Brown and Kodric-Brown 1979). Concentration varied, as at Tucson (Waser 1979), from the dilute nectar typical of hummingbird flowers to the high concentrations which the birds prefer (Pyke and Waser 1981, Stiles 1976). The sucrose-dominant composition is typical of hummingbird flowers (Stiles 1976, Freeman et al. 1984). These characteristics are obviously acceptable to carpenter bees as well.

Carpenter bee visitation was intensive enough to keep ocotillo from being a rewarding nectar source for hummingbirds in two of three seasons. Ocotillo was thus an unpredictable and ephemeral energy source (Montgomerie and Gass 1981) for hummingbirds in BBNP; ironically, it was much more consistent in its flowering between years than other hummingbird nectar sources such as *Penstemon havardii* and *Castilleja lanata* (Scott, unpublished data). Hummingbirds are probably frequent visitors to ocotillo only under restricted conditions: in the foothills habitat near localized nesting areas, when carpenter bee density is low, and when drought limits availability of such alternatives as *P. havardii.* This combination of circumstances did not occur in three seasons. I conclude that ocotillo nectar has little positive impact on the population density of hummingbirds in BBNP, and that hummingbirds are of little importance as pollinators of *F. splendens* in this part of its range. Ocotillo may even have an indirect negative effect on hummingbirds by contributing to population growth

of carpenter bees (Chapter 3), which later in the season rob nectar from other hummingbird flowers (*P. havardii, Anisacanthus linearis, Chilopsis linearis*) (see Chapter 3, Table 3.1).

Grant (1958) stated that *F. splendens* was self-compatible, citing a breeding test at Claremont, California, in which an unspecified number of plants and flowers were self-pollinated by hand. "The selfings led to a good set of seeds. The F_1 seeds yielded a healthy crop of seedlings which grew into normal individuals." However, methods and data were never presented, so the statement is unconvincing. I conducted a breeding test in San Diego County, California, in 1988 which gave results similar to those reported here for BBNP (see Chapter 4).

One of Waser's (1979) experimental treatments of ocotillo inflorescences at Tucson was enclosure in a fine mesh cage that excluded all flower visitors and tested the capacity for self-pollination. The mean number of seeds in fruits that matured on such inflorescences was low on nine replicate plants (range of means: 1.2 - 3.3 seeds/fruit) and relatively high (6.6 seeds/fruit) on one. Waser concluded that ocotillo flowers "can self-pollinate but only to a limited extent."

My results, incorporating the probability of fruit set, indicate that the capacity for self-pollination is very limited. The response to geitonogamous pollination is equally weak and probably contributes little or nothing to an ocotillo's reproductive success, because seedling establishment is a low probability event. A plant producing 2,445 flowers (the mean at Maverick in 1987) would mature 391 seeds through geitonogamous pollination. From seven years of censuses, Shreve (1917) concluded that no more than one in 10,000 seedlings at Tucson survived two summers (see also Goldberg and Turner 1986).

Self-incompatibility is common in long-lived shrubs and trees that flower profusely (open > 50 flowers per day). Most of the dominant, mass-flowering perennials of the Sonoran Desert are self-incompatible (Simpson 1977). Tropical

trees and shrubs, many of which flower profusely, are typically self-incompatible (Bawa 1974, Bullock 1985). McDade (1985) tested breeding systems of nine hummingbird-pollinated *Aphelandra* (Acanthaceae) species. Four of five species that opened only a few flowers per day were fully self-compatible (but likely to be outbred), whereas profusely-flowering shrubs were all partially self-incompatible. One hypothesis for the prevalence of self-incompatibility in mass-flowering plants is as follows. Selfed progeny may have lower fitness on average than outcrossed progeny, for various reasons (e.g., increased homozygosity may cause inbreeding depression; production of a genetically variable set of progeny may be favored). If so, and if flowers are likely to receive self pollen first but outcross pollen at some point during flower life, then evolution of incompatibility will be favored. Incompatibility allele systems allow plants to distinguish between pollen grains of different origin and genetic relatedness (Uyenoyama 1987). This combination of traits (self-incompatibility and profuse flowering) entails a risk of massive failure to set seed. If reward levels exceed the needs of the local pollinator populations, then individual foragers will need to visit fewer flowers for a given amount of nectar or pollen, and consequently may be poor vectors of outcross pollen. For a long-lived plant, the risk is perhaps an "acceptable" trade-off for the advantage of producing large numbers of outcrossed seeds in some years.

The difference between the two outcrossing treatments may indicate mild outbreeding depression (Price and Waser 1979) at a mating distance of 1 km, or may have resulted from differences in the handling of flowers. Flowers collected 1 km from experimental plants were placed in vials for 15-30 minutes before being used as pollen donors.

A large-scale failure to set seeds occurred at only one BBNP site (Maverick), in two of three years. In one year there were significant declines in fruit set and seed set at all sites, clearly related to low visitation rates by carpenter bees. Otherwise the needs

of the carpenter bee population matched or exceeded availability of ocotillo's floral rewards. This situation, highly favorable for ocotillo pollination success, reflects certain aspects of carpenter bee biology and a fortunate abundance of their nest plants (*Agave, Dasylirion,* and *Yucca* species) over most of ocotillo's elevational range. Broad distribution of the nest plants and large foraging ranges mean that bees can exploit most ocotillo populations. The ability to become inactive for weeks or months allows bees to inhabit sites where nectar and pollen are intermittently available. Foraging carpenter bees have high rates of energy expenditures (Chappell 1982), which must be offset by nectar consumption. Most importantly, females use ocotillo pollen and nectar as a food provision for offspring (Chapter 3), so their demands for both rewards are high. They provision each larval cell with approximately 525 mg of nectar sugar and 545 mg of pollen (Chapter 3). They appear to provision as many cells as possible (typically 4-9) while suitable food plants are in flower. Thus reward levels may have a profound effect on bee density, and on visitation rates in subsequent flowering seasons. The importance of ocotillo food rewards for bee populations is explored in Chapter 3.

The flowering phenology of BBNP ocotillos was similar to that of Tucson populations studied by Waser (1979). Tucson plants flowered synchronously in the spring. Flowering was delayed a few weeks during a cool wet spring (as in BBNP in 1987), but flowering duration was "remarkably consistent" between years. Flowering at each Arizona site lasted 50 - 60 days, whereas BBNP populations completed flowering in 27 - 48 days. Waser (1979) hypothesized that the timing and duration of flowering was an adaptation to a brief, predictable period of migrant hummingbird abundance at Tucson. He obtained experimental support for this hypothesis (Chapter 1), but also noted that carpenter bees tracked the flowering of ocotillo more closely than hummingbirds. In Texas, there is no evidence that the timing of flowering is related to local availability of hummingbirds. There was not a detectable wave of migrant hummingbirds through ocotillo habitat in spring; resident hummingbirds were present

before ocotillo flowered and remained for five months, but were generally scarce in the desert and rarely visited ocotillo. The timing of flowering by Texas plants was as consistent as Arizona populations and the duration shorter. I hypothesize that the timing and duration of flowering in Texas reflects adaptation to breeding carpenter bees and competition with other profusely flowering perennials (honey mesquite, *Prosopis glandulosa*, and creosotebush, *Larrea tridentata*), which most female bees at least sampled during provisioning of nests (see Chapter 3). Flowering began soon after carpenter bees became active in spring. Opening large numbers of flowers each day may be necessary to induce regular visitation by provisioning female bees and would result in a brief flowering period. The problem with testing this hypothesis is that it does not predict a particular duration or degree of profuse flowering.

Foraging patterns in 1988, when bee density was high and average floral rewards were low, appeared favorable for outcross pollination. Individuals visited many plants, but relatively few flowers per plant. Presumably, outcross pollen is most likely to be deposited on the first several flowers that a bee visits on a new plant. But patterns of pollen dispersal are potentially complex (Lertzman and Gass 1983) and need direct study (Waser and Price 1982, 1984, Geber 1985). Measurements of pollen movement by bumblebees may be relevant. Queen bumblebees visiting *Delphinium nelsonii* picked up > 340 grains at a virgin flower; when presented with a series of hand-held, emasculated flowers, the number of grains deposited decreased with position in the sequence and the median pollen grain reached the tenth flower (Waser 1988). The dispersal distance for *Mertensia ciliata* pollen transferred by worker bumblebees was similar (Geber 1985).

Flowers continued to produce nectar and receive visits after pollen had been removed from all anthers. This phase of flower life may be important for receipt of outcross pollen because no self pollen (from that flower) is present to layer over the pollen on the body of the arriving bee. Experiments with *Ipomopsis aggregata* showed

that dye particles (pollen mimics) were dispersed greater distances when hummingbirds visited flowers with empty anthers than when anthers held pollen (Price and Waser 1984).

Profuse flowering and relatively rich pollen and nectar production are probably key features which induce carpenter bees to visit *F. splendens* regularly despite the availability of other common and productive pollen and nectar sources (*P. glandulosa*, *L. tridentata*). The 14 mm-long floral tube may make *F. splendens* a more rewarding nectar source for carpenter bees than *P. glandulosa* or *L. tridentata*, whose nectar is accessible to small insects (see Simpson et al. 1977, Hurd and Linsley 1975). Several other plant characteristics may influence foraging behavior and pollen transfer. The architecture of ocotillo, with terminal flower clusters on spreading branches and much open space between them, may encourage movement between plants, although bees distinguish rewarding plants. Compact flower clusters enable bees to walk between adjacent open flowers, although they often fly. A relatively broad floral tube (4 mm diameter), stout pedicel, the exserted mass of stamens, and adjacent flowers and buds make it easy to grasp the flower and pierce the base for nectar. Carpenter bees have some difficulty grasping pendulous, slender-tubed hummingbird flowers such as *Penstemon havardii* and *Anisacanthus linearis*.

Although long enough to exclude most bees and small insects, the floral tube of Texas populations of *F. splendens* is 6 mm shorter than in California (Figure 2.10; see also Henrickson 1972), where carpenter bees are rare and hummingbirds are sometimes common visitors (Chapter 4). This may reflect a history of interaction with carpenter bees as the primary pollinator in the Chihuahuan Desert and a lack of selection for transfer of pollen via hummingbirds. The short floral tube of *F. splendens* in Texas probably reduces the effectiveness of hummingbirds, especially of the long-billed Lucifer Hummingbird (average culmen length: 21.9 $\pm$ 0.8 mm, n = 7 females; 21.0 mm, n = 1 male; data from birds netted in BBNP). Although anthers and stigmas

are exserted (positioned 25-30 mm distal to the nectar pool), the tube is wide enough that hummingbirds can thrust their bill into it along one side and make only slight contact with sexual parts. An experimental comparison of pollen deposition by carpenter bees and hummingbirds using hand-held flowers (Waser 1988) from Texas and California populations would test the hypothesis that Texas populations of *F. splendens* are adapted morphologically to *X. c. arizonensis* rather than to hummingbirds.

Chapter 3

Importance of ocotillo floral rewards for nesting of a carpenter bee pollinator [1]

1 This chapter is modified from a manuscript submitted to Ecology on 29 January 1989, co-authored by Peter E. Scott, Stephen L. Buchmann, and Mary K. O'Rourke. The pronoun "we" is used throughout.

INTRODUCTION

In plant-pollinator mutualisms, benefits to plants consist of direct effects on maternal and paternal genetic transmission. Assessing the impact of a specific flower visitor on fruit and seed set is relatively straightforward (Motten et al. 1981), although assessing paternity is more difficult. The contribution of a plant's food reward to pollinator fitness is often indirect, as when nectar is used to balance the daily energy expenditures of a hummingbird. Consequently, plant-pollinator mutualisms often are described incompletely; it is simply assumed that floral rewards are important to the pollinator. However, many plants provide resources (pollen, nectar, oils, even seeds) that pollinators use to feed offspring (Simpson and Neff 1983). The effect of a plant species on a pollinator's fecundity can be measured if one can find the pollinator's nest and identify the sources of offspring food supplies. The larval food of bees, for example, is a mixture of pollen and nectar. The pollen grains in a larval provision can be identified, although sources of nectar sugar cannot. The usefulness of nest content analysis in measuring fitness benefits to flower visitors was shown by Strickler (1979). She compared the rate of cell provisioning by specialist and generalist bee species feeding on *Echium vulgare* and found that the specialist provisioned offspring at a faster rate.

During a study of the desert shrub ocotillo (*Fouquieria splendens*) in Big Bend National Park (BBNP) in western Texas, we assessed the importance of the plant as a breeding resource for the carpenter bee *Xylocopa californica arizonensis*. Waser (1979) established that carpenter bees, along with migrant hummingbirds, were major pollinators of *F. splendens* at Tucson, Arizona. He and Henrickson (1972) observed female carpenter bees gathering pollen of *F. splendens*, suggesting its use in larval provisions. In BBNP, carpenter bees are the primary pollinator of *F. splendens* (see Chapter 2). We investigated the impact of *F. splendens* on carpenter bee fecundity using techniques that are simple but applied rarely in conjunction with pollination studies.

The nests of *X. c. arizonensis*, excavated in dead inflorescence stalks of agaves and similar plants, were easy to locate. We sampled and identified pollen from larval provisions or fecal pellets. We related the pollen and sugar requirements of a carpenter bee larva to the output of an average ocotillo plant. Results indicate that ocotillo is a major food for carpenter bee larvae. We consider population-level consequences (Addicott 1986) of the ocotillo - carpenter bee mutualism.

METHODS

During parts of four seasons (1985-1988) we recorded observations of flower usage and nesting by carpenter bees. Most records of flower usage, except in the case of *F. splendens*, were based on casual encounters rather than systematic observations throughout a plant's flowering period. In 1988 we searched intensively for nests in the foothills of the Chisos Mountains and on the outwash plains at sites where nest plants were common. All nests except one were collected between 22 April (near the end of ocotillo flowering) and 27 May. Stalks were sawed in half through the bee's entrance hole and split. Any adults in the tunnel were identified to sex. Cells contained developing larvae with partly consumed provision masses or pupae with fecal pellets. We collected some large provision masses from each nest (if any remained) and all fecal pellets. We attempted to rear some larvae and all pupae, or their parasites; afterward, provision remnants or fecal pellets were collected. We also collected the small amount of pollen and nectar mixture that was plastered outside the last-made cell of most nests.

To determine the relative importance of different pollen types as provision material, we hydrated and mixed provisions and fecal pellets (keeping each nest separate), extracted a 10-20 microliter subsample, and prepared a microscope slide using methods similar to Kapp (1969: 11). We identified a minimum of 500 pollen grains from each bee nest at 1000X magnification. Unknown pollen types were compared with reference material curated in the Department of Geosciences, University

of Arizona. Because the quantity of nutrients available to a consumer probably increases with pollen grain volume (Simpson and Neff 1983), we calculated the volumes of three taxa common in nests and the percentage of pollen volume accounted for by each. We assumed that volumes of the different taxa were proportional to mass by a constant factor.

All provisions from BBNP nests were used in the analysis of pollen type frequency. We used intact provisions of *X. c. arizonensis* collected near Tucson, Arizona in 1987 and 1988 to estimate the total quantities of pollen and nectar sugar required by a carpenter bee larva. Provisions were individually dried at 60^{o} C for 24-48 hours until they reached a constant mass. The mass and composition of sugars in four dried provision samples were determined using standard methods of gas-liquid chromatography. The difference between the original dry mass of the sample and the mass of nectar sugars was attributed to pollen.

We counted the number of flowers produced annually by ocotillos in BBNP and measured daily nectar production (see Chapter 2). We measured pollen production by ocotillos at Tucson. Flower buds were collected from two plants, undehisced anthers were cracked open, and pollen was removed with a fine brush and weighed on a Mettler balance.

RESULTS

Carpenter bee density appeared greatest in the mountain foothills and on the upper outwash plains, where at least three nest plant species and a succession of nectar and pollen sources (Table 3.1) were usually present. We also found old nests of *X. c. arizonensis* along the banks of the Rio Grande (670 m) and as high as 1700 m in the Chisos Mountains, a range that encompasses almost all the park's ocotillos. Sixteen active nests were collected in 1988 at seven sites (Figure 3.1) from stalks of *Dasylirion leiophyllum* (n = 11), *Agave lechuguilla* (n = 3), and *Yucca elata* (n = 2).

Females also used stalks of *Agave havardiana*, which are larger than other species. At sites where active nests were found and elsewhere, many suitable stalks of *D. leiophyllum*, *A. lechuguilla*, and *Y. elata* lacked carpenter bee tunnels. Only *A. havardiana* was used fully.

Most nests consisted of a linear sequence of cells at one end of a tunnel 12-45 cm in length. In three stalks there were two sequences of cells, one at either end of the tunnel. Fourteen nests were complete when collected (provisioning had ceased); they contained 6.0 $\pm$ 3.1 provisioned cells ($\tilde{x} \pm$ S.D., range 1-11), and were tended by one (n = 11) or two adult females.

Fouquieria splendens and honey mesquite, *Prosopis glandulosa*, together accounted for > 50% of the pollen grains in each spring nest sample and for > 90% in 14 of 16 nests (Figure 3.2). Most of the remaining pollen was identified as belonging to the family Zygophyllaceae: either creosotebush, *Larrea tridentata* (most likely), or guayacan, *Guaiacum angustifolium*. Each nest contained pollen from at least two, usually three sources (disregarding sources that accounted for < 1.0%). Ocotillo grains predominated in nine nests, mesquite in six, and Zygophyllaceae grains in one. Ocotillo pollen had a greater volume (17.52×10^{-9} cm^3) than either mesquite (8.55×10^{-9} cm^3) or Zygophyllaceae pollen (2.60×10^{-9} cm^3). In terms of volume, ocotillo predominated in 13 nests and accounted for 69% of an average nest sample (Table 3.2).

Provisioning ceased when ocotillo finished flowering. During searches for nests in May, no pollen-gathering females were seen, no incomplete nests were found, and few bees foraged. A few adults robbed nectar from *Chilopsis linearis*, which flowered sparsely. Females stayed in nests with developing broods; some males were found in old nest stalks. Bees collected as larvae or pupae eclosed as adults almost synchronously, suggesting that nests were provisioned during a brief period. Twenty bees from 11 nests eclosed between 8 and 17 June; three others eclosed later, the last on 10 July. In other years, as in 1988, carpenter bees had a distinct spring provisioning period that ended

when ocotillo finished flowering (Table 3.1). In May of those years, bees were either inactive or robbed nectar from *Penstemon havardii* and *Chilopsis linearis*. During the summer rainy season they foraged intermittently and sometimes nested. In 1986 many females gathered pollen from *Larrea tridentata* (June - July) and *Agave lechuguilla* (July - August). A single freshly provisioned nest was collected on 1 July. Its pollen composition was 92% Zygophyllaceae (probably *L. tridentata*), 6% Liliaceae (probably *Dasylirion leiophyllum*), and 1% *Agave* sp.

During searches for nests, three cases of predation on larvae by Ladder-backed Woodpeckers (*Picoides scalaris*) were recorded. Woodpeckers pecked holes in stalks at the level of cells and apparently extracted the pollen and nectar food masses as well as bee larvae. Contents of all three cells in one stalk were consumed, three of four in another, and five of seven in another. In addition, four of 16 broods lost one or more young to parasitism by the larvae of a beefly (*Anthrax xylocopae*) or a meloid beetle (*Cissites aurantiirostris*).

An average ocotillo plant in BBNP produced 2,204 flowers in 1988 (overall mean of 30 plants, 10/site; see Chapter 2, Figure 2.6). Nectar production per flower ranged from 1.1 to 4.6 mg sugar at four sites (Chapter 2, Table 2.5, Figure 2.7). The average of the four site means was 2.6 mg sugar/flower. Flowers buds from Arizona ocotillos contained a fresh mass of 4.6 $\pm$ 0.5 mg pollen ($\bar{x} \pm$ S.D., n = 10). We assume that the fresh mass contained 25% moisture and would be equivalent to 3.4 mg in dry mass.

Intact provisions of *X. c. arizonensis* collected in Arizona had a dry mass of 1.07 $\pm$ 0.26 g (n = 115). Sugars (primarily fructose and glucose) comprised 48.9% of the mass (range: 44-55%, n = 4 determinations). We estimate that an average provision contained 525 mg sugar and 545 mg pollen. Assuming that BBNP provisions contained the same mass of pollen as Arizona provisions, we estimate that an average larval provision from the spring 1988 nests contained 376 mg of *F. splendens* pollen (545 mg

x 0.689, the proportion of *F. splendens* pollen by volume). Thus 111 flowers would yield the amount of *F. splendens* pollen supplied to each larva. We could not associate the sugar in provisions with particular nectar sources; however, bees gathering pollen from *F. splendens* also robbed nectar. If *F. splendens* nectar were the sole source, 202 flowers would supply enough sugar for one provision. An average ocotillo in 1988 produced an estimated 7.5 g pollen and 5.7 g nectar sugar, supplying enough pollen for about 14 carpenter bee larvae (if bees used only *F. splendens* pollen) and enough nectar for about 11 larvae.

DISCUSSION

The large quantities of pollen and sugar required by a carpenter bee larva restrict breeding to periods when pollen and nectar are plentiful. Plants used in BBNP were common, mass-flowering perennials. Carpenter bees capitalized on these relatively brief but rich flushes of food. Calculations relating provision content to floral rewards give an idea of ocotillo's potentially enormous impact on the density and growth rate of the carpenter bee population. The average plant produced more pollen and nectar than needed to provision an average carpenter bee brood of six larvae. In theory, if the starting density of carpenter bees in spring were one female per mature ocotillo plant (or less), ocotillo could fuel a several-fold increase in population density. Most nectar and pollen produced by ocotillos was harvested by carpenter bees in 1986 and 1988 (Chapter 2), when their density was high and their efficiency discouraged other visitors. The net change in density due to spring breeding was not determined. Predation and parasitism of developing broods appeared to be common. But it is clear that carpenter bees have the potential to convert the three-to-four-week spring flush of pollen and nectar into several-fold population gains.

Would changes in numbers of ocotillos lead to changes in carpenter bee density (Addicott 1986)? Almost certainly: ocotillo was the most heavily used spring larval

food, and bee density was high enough in two of three seasons to thoroughly crop the rewards made available by ocotillo (see Chapter 2, Table 2.9). We infer from this that spring brood size in those years was limited by food availability, and that brood size would have been lower had fewer ocotillos been available.

The ability of *X. c. arizonensis* to nest in old stalks of *Agave lechuguilla*, the "indicator plant" of the Chihuahuan Desert (Powell 1988), should mean that nest sites are not limiting at most Chihuahuan Desert sites. An abundance of potential nest plants is probably important in reducing woodpecker predation, to which a developing brood is vulnerable for approximately 50 days.

Ocotillos have high seed set as a result of high visitation rates of carpenter bees (Chapter 2) and therefore should benefit from their own effect on bee density. However, nine months elapse between maturation of young bees from spring broods and the next flowering of ocotillo. High densities at the beginning of ocotillo flowering depend, perhaps critically, on summer floral resources, which provide energy reserves for overwintering and support a second breeding episode. The summer breeding resources -- *Larrea tridentata*, *Agave lechuguilla*, and possibly *Dasylirion leiophyllum* -- are probably pollinated by carpenter bees. If so, then these plants may be "effective mutualists" of spring-flowering ocotillo and mesquite, each set of plants helping to maintain a common pollinator at high density (Waser and Real 1981). *Larrea tridentata* also competes with ocotillo when it flowers in spring.

The number of carpenter bee cuts on flowers (Chapter 2) may be a good index of changes in bee density between years, because the number of flowering ocotillos changed little, flower production varied less than two-fold between years, and carpenter bees concentrated on ocotillo while it flowered. Judging from cuts on flowers, bee density in April was highest in 1986, low in 1987, and high in 1988 (Chapter 2, Table 2.8). That any gains following the 1986 ocotillo flowering period disappeared prior to flowering in 1987 indicated the importance of other factors, i.e., possibly an inadequate

energy supply later in the year, combined with a cold spring that prolonged the inactive season and caused starvation. On the other hand, ocotillo may have contributed to the increase from 1987 to 1988. We speculate that carpenter bee density fluctuates widely around a high mean. High densities are frequently attained because of a nearly unlimited supply of nest sites and the ability to capitalize on short-term flushes of pollen and nectar. Because ocotillos are long-lived (Goldberg and Turner 1986), seasons of low seed set (due to a carpenter bee population crash) should have no effect on the density of mature plants, especially if seasons of high seed set are at least as frequent (Chapter 2). Reliable annual flowering by ocotillo should help carpenter bees rebound from low densities.

For an ocotillo population, the consequences of supporting a high density of carpenter bees include the production of many seeds and presumably (Shreve 1917) germination of many seedlings. Seedling establishment is severely limited, occurring on the order of once per 10,000 germinations (Shreve 1917). It is not clear whether a high density of carpenter bees affects population growth or equilibrium density of ocotillo, i.e. whether a greatly increased number of germinations each year affects the number of adult plants recruited per century. However, individual fitness would likely be maximized by maximizing annual seed production, as long as survival is not compromised. Therefore, adaptation to carpenter bees should be favored when conditions allow ocotillo to exert its positive effect on bee density. The necessary conditions are an abundance of nest sites and a flush of floral rewards later in the year; a continual supply of floral rewards in the habitat is not required. Several traits of Texas populations of *F. splendens* may reflect adaptation to carpenter bees. The brief period of massive flowering may have evolved because it attracts breeding carpenter bees and induces intensive visitation. The "brush" morphology (Stiles 1981) and short tube of Texas ocotillo flowers (see Chapter 2) may make them easy for carpenter bees to handle and

increase their efficiency as pollinators. Carpenter bees show no evidence of adaptations specific to *F. splendens*.

The interaction between *F. splendens* and *X. c. arizonensis* in BBNP can be characterized as a mutualism in which the pollinator frequently attains a high enough density to harvest floral rewards completely, leading to excellent outcrossing service and high seed set for the plant. This is predicted to be a logical outcome of interactions between plants and pollinators (Montgomerie and Gass 1981), but many factors can prevent pollinator populations and plant reward levels from equilibrating. California populations of *F. splendens*, for example, are poorly pollinated. Hummingbirds, orioles, and carpenter bees harvest only a small percentage of its nectar and pollen there, except during occasional periods when migrant hummingbirds and orioles are abundant (see Chapter 4). Successful functioning of the ocotillo - carpenter bee mutualism in BBNP is due to several factors which help maintain a high bee density: use of ocotillo rewards as a larval food, availability of other floral rewards in summer, a fortuitous abundance of nest sites, and the ability of bees to reduce energy expenditures during lean periods.

Chapter 4

Pollination ecology of ocotillo in the northwestern Sonoran Desert

INTRODUCTION

I studied the pollination of *Fouquieria splendens* in San Diego County, California during parts of two flowering seasons. Objectives were (1) to determine the relative importance of hummingbirds, carpenter bees, and other potential pollinators; and (2) to compare flowering behavior and breeding system with the characteristics of Texas populations. Availability of hummingbirds was expected (Chapter 1) to be greater than in the Chihuahuan Desert and possibly different from patterns at Tucson, Arizona (Waser 1979). Costa's Hummingbird (*Calypte costae*) breeds in the desert scrub of the western Sonoran Desert in late winter and spring, and Rufous Hummingbirds (*Selasphorus rufus*) migrate northward through the region in March and April (Garrett and Dunn 1981). Carpenter bees (*Xylocopa californica arizonensis*; the same taxon as in western Texas) were known from several sites in southern California (Hurd 1955, Hurd and Linsley 1959, Chappell 1982), but Hurd (1955) termed their distribution "widely discontinuous." Henrickson (1972: 514) reported that carpenter bee cuts on ocotillo flowers at western sites were "much less frequent" than in the Chihuahuan Desert.

At the suggestion of J. Henrickson and N. M. Waser, Anza-Borrego Desert State Park (ABDSP) was selected as an area having extensive stands of ocotillo. M. Jorgensen and N. M. Waser recommended study sites within the park. The park extends from 5 to 90 km north of the border with Baja California, Mexico and protects over 600,000 acres, including much desert scrub habitat. It is in the Lower Colorado River Valley province of the Sonoran Desert (Turner and Brown 1982). Annual rainfall at park headquarters (240 m) near Borrego Springs averaged 178 ± 87 mm (± S.D.) between

1962 and 1987 (data from The Borrego Sun, issue of 2 February 1989). On average, 68% of the yearly total falls between November and March.

METHODS

Methods were similar to those used in Texas (Chapter 2). I concentrated on measuring natural visitation rates at a variety of sites, by direct observation and by inference from flower condition and reward levels. During intensive visitation by Rufous hummingbirds, I studied characteristics of territories and foraging patterns within them.

In March 1987 I marked 20 ocotillo plants at four sites on rocky outwash slopes. From north to south, the sites were Desert Gardens (270 m), Glorietta Canyon (450 m), Mescal Bajada (450 meters elevation), and Bow Willow (300 m); the last site was 60 km south of Desert Gardens. *Justicia californica* (Acanthaceae), a shrub commonly visited by hummingbirds, was common except at Desert Gardens. At Glorietta Canyon 20 *J. californica* plants were marked. In 1988 I established another ocotillo plot at Mountain Palm Springs, 4 km north of Bow Willow, after discovering that carpenter bees were restricted to the vicinity of palm groves. Flowering phenology was checked at intervals of one to two weeks. The *Justicia* plot was checked only in 1987.

I tested the breeding system of *F. splendens* and the effectiveness of natural pollinators at Desert Gardens in 1988. I used four plants and three treatments, each applied to a separate inflorescence on each plant. Treatments were (1) self (geitonogamous) pollination by hand; (2) outcross pollination by hand; and (3) open pollination. Methods differed from the Texas breeding test (Chapter 2) in that hand-pollination treatments were applied twice daily during the first three days of treatment, and two to four donors were used in the outcrossing treatment instead of one. In the morning (9-11 March), each outcrossed flower received pollen from two neighboring plants, one on the north and one on the south side of the plant; in the afternoon, donors

from the east and west were used. From 12-17 March treatments were applied once daily except on 15 March (no treatment), with the locations of outcross donors alternating on successive days. Flowers remained open for two to three days. Flowers that opened before 9 March on treated and control inflorescences were cut, as were all buds remaining on 17 March. I collected fruits on 14 April.

In both years, I obtained limited data on natural pollination success at ABDSP because I departed in late March to observe the full flowering season in Texas. I could determine whether a fruit was developing 10-15 days after a flower opened, although measurements at this stage probably overestimated the percentage of flowers that matured fruits. Seed set could not be determined until 25-30 days post-flowering. In 1987 fruit set was determined for flowers that opened between 1 and 16 March on marked inflorescences. Buds, flowers, finished flowers, and fruits were counted once weekly. The final count was made on 30 March. No data on seed set were obtained in 1987. In 1988 I returned in mid-April and determined fruit set and seed set for flowers that had opened between 6 and 18 March.

RESULTS

Flowering phenology

Most ocotillo populations in Anza-Borrego flowered for at least 6 weeks (Tables 4.1, 4.2), 2-3 weeks longer than Texas populations. They showed more variability in the duration of flowering than Texas populations, and advanced more slowly to a peak of massive flowering. Still, most flowers opened during a 3-4 week peak in late March or April. During peak flowering, large California plants had as many as 300-700 flowers open at one time. Variability was greatest at Bow Willow: in 1987, flowering may have continued for 3 months (note number of inflorescences finished on 28 February and in bud on 30 March, Table 4.1), whereas in 1988 flowering lasted 7 weeks. The Glorietta Canyon population, located on a north-facing slope, flowered latest and in 1988 had the

shortest flowering period: almost all flowers opened between 22 March and 14 April (Table 4.2).

Justicia californica flowered steadily throughout March 1987 at Glorietta Canyon while the adjacent ocotillos remained in bud. The average plant had 37.9 ± 25.2 flowers on 8 March and 44.2 ± 37.3 flowers (± S.D.) on 22 March. *Justicia californica* may begin flowering earlier than *F. splendens* at other sites also; it appeared to be flowering well in early March at most sites. However, there was much overlap in the flowering periods of the two species. Many *Agave deserti* flowered in March 1987, attracting Rufous Hummingbirds; few flowered in March 1988.

Inflorescence production

Populations of *F. splendens* showed only minor (less than two-fold) variation in inflorescence production between years (Figure 4.1)

Flower visitation by hummingbirds, orioles, and other birds

I observed pollinator activity at *F. splendens* plots from 3 to 28 March 1987 and from 6 to 21 March 1988. This was prior to peak flowering at most sites; typically, plants had five to ten inflorescences in flower. However, at Desert Gardens I made observations at a site (1 km from the plot where phenology was recorded) where flowering peaked in mid-March both years.

In 1987, visit rates were low in the first half of March, increased dramatically during a week when migrant Rufous Hummingbirds were abundant, then declined sharply (Table 4.3). Between 3 and 12 March, resident Costa's were seen at ocotillo flowers on several occasions but only once during a planned observation period; they did not come close to harvesting the available nectar. Bagged flowers produced 4.2 microliters and 1.5 milligrams of sucrose-equivalent sugars in 24 hours (Table 4.4). Mean standing crops > 6 microliters on March 3, 5, and 12 suggested that the average flower was

visited less than once a day by hummingbirds or other nectar consumers. Costa's also visited *Justicia californica*. Standing crops of *J. californica*, like those of *F. splendens*, were high prior to and after the passage of Rufous Hummingbirds, indicating low visit rates by Costa's. On Mescal Bajada, flowers of *J. californica* contained 4.0 ± 0.4 microliters and 1.6 ± 0.2 mg sugar (x ± standard error, n = 40) on 5 March, and 7.9 ± 0.7 microliters and 3.8 ± 0.4 mg sugar (n = 30) on 28 March (compare levels in *F. splendens* on these dates, Table 4.3). In short, the available supply of nectar sugar in *F. splendens* and *J. californica* flowers during most of March greatly exceeded the energetic needs of the local breeding population of hummingbirds.

Data from five nests and observations of fledglings (Table 4.5) suggest that most Costa's Hummingbirds initiated nests in early March and fledged young in mid-April. Nests were located in washes where flowering *J. californica* was abundant or on slopes were flowering *F. splendens* was common. Some male Costa's defended territories of ocotillo for a few hours or days, perching on conspicuous plants. Courtship flights frequently took place in stands of flowering ocotillo. One female Costa's initiated a second clutch in mid-April while feeding two fledglings (Table 4.5). She and the fledglings visited ocotillo flowers; ocotillo was near the end of its flowering period and *J. californica* was finished.

Northward-migrating Rufous Hummingbirds, first seen on 3 March 1987, were briefly common from 6 to 8 March at Glorietta Canyon in a rich patch of *J. californica* (7 male Rufous; 1 male Allen's also present). Rufous became abundant between 20 and 26 March 1987, especially at Desert Gardens (Table 4.3) and Mescal Bajada. There was much stormy weather at this time (rain on 15, 16, 22, and 24 March), and birds delayed migrating. As is characteristic of *S. rufus* (Cody 1968, Stiles 1973), individual males and females defended territories of *F. splendens, J. californica*, or *Agave deserti* against conspecifics and against Costa's hummingbirds. At Desert Gardens I censused an area approximately 300 m x 100 m containing 101 large ocotillos with

2140 inflorescences in flower and no other nectar sources. Eighteen Rufous Hummingbirds (7 males, 11 females) defended territories and 6 Costa's (3 males, 3 females) foraged in this area on 23 March. A few recognizable females stayed on territories for three days. Two were seen departing from territories in early or mid-morning after 1-3 hours of intensive feeding. They spiralled upwards for approximately 100 m, then flew to the north or northwest out of sight, and did not reappear on territories in the next hour. Territories included > 1300 flowers, producing in excess of 2 g sugar (Table 4.6), the approximate quantity needed by a 3-gram hummingbird to meet 24-hr energy expenditures (Montgomerie 1979); some nectar was lost to orioles. Birds spent most of the day within territories, flycatching as well as taking nectar. Visit rates by the territorial Rufous and by intruding orioles were high (Tables 4.3), which kept nectar availability low (0.5-1.5 microliters). At Mescal Bajada on 22 March, I observed 32 Rufous (23 males, 9 females) and 7 Costa's (6 males, 1 female) on a 2-hour walk. These birds were more dispersed than those at Desert Gardens and fed at *F. splendens*, *J. californica*, and *A. deserti*. After the weather cleared, migrant Rufous departed, visitation rates to ocotillo dropped, and increasing volumes of nectar accumulated (Table 4.3, March 27-28).

Rufous Hummingbirds defending ocotillo territories spent the day moving between few plants and often visited a long series of flowers before moving to a neighboring plant. They visited many more flowers at each plant (Figure 4.2) than did carpenter bees in Texas (Figure 2.10), and usually only one or two plants per foraging bout. Such a pattern could result in poor outcrossing service, despite the high visitation rate; unfortunately, pollination success during this period was not determined. Hummingbirds contacted anthers and accumulated pollen on the facial feathers and bill during a bout; between bouts, birds sometimes cleaned themselves of pollen by scratching with a leg.

Three species of orioles were common visitors to ocotillo in 1987 (Scott's Oriole, *Icterus parisorum*; Hooded Oriole, *I. cucullatus*, and Northern (Bullock's) Oriole, *I. galbula bullocki*). Orioles landed on stems, walked onto inflorescences, probed flowers vigorously, and accumulated pollen on the bill, forecrown, and chin. They mainly sought nectar and occasionally nibbled pollen. Insertion of the bill split the flower tube along one side. I quantified visitation using this sign. On several dates, > 25% of flowers in random samples had been probed by orioles. Apart from splitting corolla tubes, orioles did not appear to damage the flower; the ovary is probably protected from oriole bills by the mass of trichomes at the base of stamen filaments (Henrickson 1972). Orioles tended to spend a long time in each plant, and therefore may have been poor vectors of outcross pollen.

Other birds visited occasionally but were not potential pollinators. House Finches (*Carpodacus mexicanus*) destroyed flowers by plucking them and munching the base of the corolla. Verdins (*Auriparus flaviceps*) punctured corollas at the base. Yellow-rumped Warblers (*Dendroica coronata audubonl*) explored inflorescences in search of solitary spiders; they never probed or pierced flowers. Orange-crowned Warblers (*Vermivora celata*) also searched for spiders; although they slit flowers of *J. californica* to rob nectar, they did not do so on *F. splendens*.

In 1988, hummingbirds visited at such low rates that they were recorded only once during six planned observation periods between 6 and 21 March (Table 4.7). The impressive wave of migrant Rufous seen in 1987 did not materialize, although a few were seen. No storms occurred. During many hours spent among ocotillos carrying out the breeding test, I observed Costa's or Rufous visit 20-40 flowers on several occasions, but they had little impact on the nectar supply (Table 4.7). For more than two weeks, the average ocotillo flower contained at least 4 mg of nectar sugar, well above the 24-hour production rate (1.5 mg, measured in 1987). Migrant orioles were rarely seen and did not visit ocotillos (Table 4.7).

Carpenter bees

Carpenter bees were rare or absent at most Anza-Borrego sites. In 1987 I observed a carpenter bee visit ocotillo only twice. Flower cuts indicated a low and intermittent rate of visitation, highest at Bow Willow (Table 4.3). In 1988 there was again little or no sign of carpenter bees at most sites (Table 4.7). However, in two groves of palms (*Washingtonia filifera*) at Mountain Palm Springs (4 km from Bow Willow) I found approximately 50 bees active between 12 and 22 March. I collected one male and identified it as *Xylocopa californica arizonensis*. Males hovered around hanging fronds high on the palm trunks and chased each other and an occasional pollen-laden female returning to the palm. Female *X. c. arizonensis* apparently nest in the stems of old palm fronds in these groves, as they do at Joshua Tree National Monument, San Bernardino Co., California (O'Brien and O'Brien 1963). The bees at Mountain Palm Springs visited flowers of *F. splendens* and *Larrea tridentata* on slopes adjacent to the palm groves, but not intensively. Ocotillo flowers near Palm Bowl grove had 1.2 $\pm$ 0.8 cuts/flower ($\bar{x}$ $\pm$ S.D., n = 30) on 12 March and 0.9 $\pm$ 0.8 cuts/flower (n = 40) on 19 March. At Surprise Grove, 2 km distant, only 1 of 30 flowers was cut on 19 March (Table 4.7). All visits I observed were by males, which pierced for nectar and were passively dusted with pollen. Males appeared to have no difficulty obtaining nectar from the flowers, although tubes averaged 6 mm longer than Big Bend flowers.

I searched for nests of carpenter bees in dead flower stalks of *Agave deserti*, which are common on the bajadas of Anza-Borrego at most sites where ocotillo occurs. The stalks are 6-12 cm thick and 2-3 m long, similar to *Agave havardiana*, the favorite nest plant of carpenter bees in Big Bend. I examined 20 stalks on Mescal Bajada and 50 near Agua Caliente; none had carpenter bee tunnels. Tunnels and exit holes of cerambycid beetles were present in 35% and 48% of the stalks. *Xylocopa californica arizonensis* appears to use only palms as nest sites in Anza-Borrego. The palms grow only in well-watered canyons.

Pollination success and breeding system

In 1987, few flowers opening in the first half of March set fruits (Table 4.8). At Mescal Bajada, where no pollinators were seen on 5 or 12 March (Table 4.3), none of the 883 flowers opening on 20 marked inflorescences set fruit. At Bow Willow, only 2 of 5 plants had > 2% fruit set. I was unable to determine how effectively hummingbirds and orioles pollinated flowers during the ten days of intensive visitation in late March.

In 1988, fruit set at Bow Willow during the first two weeks of March (Table 4.9) was higher than in 1987, although no pollinators were seen on 6 or 13 March. Seed set was low.

The breeding test at Desert Gardens established that plants are self-incompatible to at least as great a degree as Texas ocotillos (Chapter 2), and are able, when outcrossed, to mature into fruits and seeds a high proportion of their flowers and ovules. Hand-outcrossed flowers matured 100 times as many seeds per flower as hand-selfed flowers (Table 4.10), and 18 times as many seeds as controls accessible to natural pollinators. Rufous and Costa's hummingbirds were the only visitors seen during the treatment period, and were rare (Table 4.7). Fruit set and seed set of controls were similar to open-pollinated flowers at Bow Willow. I conclude that inadequate pollinator service caused the very low values of fruit set and seed set in the first half of March of both years.

DISCUSSION

The absence of carpenter bees (at most sites) combined with reliable flowering behavior by *F. splendens* and *Justicia californica* means that a predictably rich supply of nectar exists for hummingbirds in the desert scrub of ABDSP in March. Yet densities of hummingbirds were not sufficient to crop the nectar supply, except when storms caused a pile-up of migrant Rufous Hummingbirds. The low density of Costa's

Hummingbird is surprising, because Costa's breeds in this habitat and should be able to convert a sustained energy flush into population gains. Costa's probably experience a superabundance of nectar during the March-April breeding period, except when Rufous are abundant; at such times, adequate nectar can probably be obtained by "itinerant foraging" at scattered nectar plants (Montgomerie 1979), because Rufous tend to aggregate in rich areas (Stiles 1973). However, the reproductive rate of Costa's, like other hummingbirds, is limited by clutch size (2 eggs) and a 7-8 week nesting cycle. This low intrinsic rate of increase and an unknown rate of nest predation may partly explain the low density of Costa's relative to the March nectar supply. Possibly the population is limited by shortages of available nectar in other months. Most Costa's emigrate from the southern California desert scrub by June and return in February (Garrett and Dunn 1981). Possibly the Borrego Desert population migrates to chapparal and coastal sage scrub habitats; Costa's are found in those habitats from March to September, breeding mainly in May and June (Stiles 1973).

Rufous Hummingbirds did indeed crop ocotillo nectar closely between 20 and 26 March 1987, but only while stormy weather discouraged northward migration. The normal daily density of migrant Rufous in March, especially in 1988, did not depress the nectar supply much. Stiles (1973) found that abundance and peak dates of spring migrant Rufous varied markedly between years in coastal chapparal habitat north of Los Angeles. Migrant hummingbird abundance also varied markedly between years in ocotillo stands at Tucson, Arizona (Waser 1979), where the Black-chinned Hummingbird was the principal species. Hummingbirds were four to seven times more abundant in one year than in three others, and even in that year were common for only half of the flowering period.

There has been less study of Rufous Hummingbirds on their migration northward through coastal and desert lowlands (Cody 1968, Stiles 1973) than of postbreeding southbound migrants in the mountains of the western United States (Gass et al. 1976,

Kuban 1977, Kodric-Brown and Brown 1978, Waser 1978, Carpenter et al. 1983). Their impact as pollinators may be different in spring. Total numbers of Rufous moving north are no doubt lower than the numbers migrating south from breeding grounds. Northbound adults may be less likely to delay along the way and feed on rich nectar supplies than postbreeding birds, especially juveniles. Cody (1968), Stiles (1973), and I, observing Rufous in spring in different southern California habitats, have each described brief periods of social territoriality in stands of *Isomeris arborea, Ribes speciosum,* and *Fouquieria splendens,* respectively. Stiles (1973) and I observed marked variation between years in abundance of Rufous that was unrelated to local availability of nectar. In contrast, southbound Rufous are usually common for 4-6 weeks in July and August in mountains of northern and southern California (Gass et al. 1976, Carpenter et al. 1983), Colorado (Waser and Real 1979), Arizona (Kodric-Brown and Brown 1978), and Texas (Wauer 1973, Kuban 1977).

The disparity between energy production by *F. splendens* in the Borrego Desert and local nectarivore demand contrasts with Montgomerie's and Gass's (1981) report that hummingbird densities closely tracked energy availability in a temperate montane and a tropical lowland habitat. Montgomerie and Gass (1981) recognized factors that could result in an imbalance between energy production and hummingbird density, including competition with nectar-feeding insects and unpredictable flowering flushes. None of the factors they listed seems applicable to the ocotillo-hummingbird interaction in the Borrego Desert, where the energy supply during March and early April is predictably high and competition from bees is unimportant, except perhaps near palm groves. They did not discuss the low rate of increase or the vulnerability of hummingbirds to brief energy shortages, a combination which I consider likely to cause nectar surpluses in hummingbird flowers.

Montgomerie and Gass (1981) argued that plant-pollinator mutualisms should favor the evolution of complete resource use, in part because it is likely that the fitness

of plants is maximized when pollinators completely harvest floral rewards. Outcrossing service is likely to be good, and energy saved by an economical output of rewards can be allocated in other ways that may increase survival and future reproductive success. According to the argument, either well-fed pollinator populations will increase to a point at which they harvest all rewards, or selection on plants will reduce excessive reward production. However, success in attracting pollinators depends on the competitive environment: a strategy of offering modest rewards may be vulnerable to a more productive genotype or species (Waser 1983: 260). The nectar surpluses and low seed set described in this chapter could result from competition between long-lived perennials for pollinators whose density is limited by factors other than the food those plants provide. Woody perennials such as ocotillo and *J. californica* can apparently store enough energy between flowering episodes and flower massively each year without compromising their survival (for > 70 years in *F. splendens*; see Goldberg and Turner 1986). If such plants are at least as successful in setting seed as plants that produce fewer flowers per day or less nectar, then there will be no genetic feedback selecting for a flower and nectar production strategy that would be more efficient on a population level, as there might be in a population of short-lived herbaceous plants. Profuse-flowering genotypes may be more successful during occasional periods of high pollinator density. The hypothesis that profuse flowering is favored, even when pollinator density is limited or highly variable, could be tested by comparing total seed set of plants that vary in flower production (Geber 1985).

The consequences of profuse flowering are quite different for California populations of *F. splendens* than for Texas populations, which interact primarily with carpenter bees. Seed production is probably much lower on average and more variable between years in California than in Texas. Although *F. splendens* is common in both regions, its population dynamics (e.g., the number of germinations and number of seedlings recruited per year) are probably different as a result of difference in

pollinator service. In Texas, the prediction of Montgomerie and Gass (1981) was fulfilled: carpenter bees usually attained a density at which they completely harvested nectar and pollen production by ocotillo (Chapter 2). This was because carpenter bees efficiently converted ocotillo food rewards into offspring, nest sites were abundant, and carpenter bees can survive on periodic floral flushes (Chapter 3).

The distribution of carpenter bees is curiously restricted in southern California; apparently, this population of *X. c. arizonensis* requires palms as nest plants. *Washingtonia* palms have occurred in southern California since the Miocene (Ray Givens, pers. comm.) and may have been widespread in the Quaternary. It is puzzling that carpenter bees do not now nest in stalks of *Agave deserti,* which would allow them to occupy greater areas of desert scrub habitat. Possibly the lengthy hot dry season and lack of a dependable summer flowering period keep densities low. Ocotillo populations adjacent to palm groves deserve study throughout an entire flowering season to see if flowering behavior and pollination success differ from populations that are remote from carpenter bees. Likewise it would be interesting to learn whether ocotillo is a larval food for palm-nesting bee populations, for this would indicate the potential for a strong mutualism, as exists in Texas.

Waser's (1979) hypothesis that ocotillo should time its flowering to coincide with migrant hummingbird passage is relevant in southern California, given the rarity of carpenter bees and the occasional high density of migrant Rufous. Although Costa's Hummingbirds are available from February through May (Garrett and Dunn 1981), hummingbird visit rates were highest by far when Rufous were abundant. Consistent with Waser's (1979) hypothesis, flowering peaked in late March or April, during migration of Rufous Hummingbirds; but flowering in ABDSP populations continued for a longer time and was more variable between years than in Tucson (Waser 1979) or Texas (Chapter 2). Several factors may affect flowering time in southern California. If migrant Rufous become abundant only during stormy periods, as my data suggest, then

their peak availability (in years in which there is a significant peak) may vary by a few weeks, resulting in inconsistent selection for flowering date. It is also possible that Costa's Hummingbirds sometimes visit frequently enough to be effective pollinators before or after the passage of Rufous Hummingbirds. Visitation by Costa's might select for low-level flowering over a longer period. Competition with *J. californica* for hummingbirds may affect flowering time (Waser 1978). *Justicia californica* begins flowering earlier than *F. splendens*, but there is much overlap. More data are needed for both species on flowering activity, visitation rates, and pollination success over entire flowering seasons. One other factor of potential importance is abiotic: flowering of *F. splendens* in southern California occurs at the end of the winter rainy season, whereas Tucson and especially Texas populations flower late in their dry seasons.

The 20 mm-long corolla tube of California ocotillos (see Chapter 2, Table 2.17), suggests that selection for pollination by hummingbirds has been stronger in California than in Texas. Long and narrow tubes are typical of hummingbird flowers, and appear to increase the probability that pollen will be transferred to or from the bird (Feinsinger 1983). There is an energetic reason for inserting the bill as far as possible into a long-tubed flower: it minimizes tongue extension and the time required to extract nectar (Montgomerie 1984). Bill lengths (total culmen) average 17.8 mm and 18.5 mm in male and female Costa's Hummingbirds, and 17.3 and 18.9 mm in male and female Rufous Hummingbirds (Stiles 1973). My observations and photographs in Tyrell and Tyrell (1985) indicate that Costa's and Rufous accumulate ocotillo pollen on the bill and on facial feathers. Two other species of *Fouquieria, F. macdougalii* (range: Sonora, Sinaloa) and *F. diguetii* (Baja California), have flower tubes that are 18-26 mm and 20-25 mm long, respectively (Henrickson 1972). In other aspects of inflorescence and flower structure, these species appear to be more specialized for hummingbird pollination than *splendens*, but their pollination ecology has not been studied.

Chapter 5

Summary

This study focussed on interactions between ocotillo and its pollinators, whose availability varied across the plant's broad range. The most interesting finding was that ocotillo is engaged in a strong mutualism with carpenter bees in Texas, but interacts weakly with hummingbirds and orioles in California. The divergent outcomes show that the link between the floral reward levels of a single plant species and the population density of its pollinator(s) is tenuous, and depends on various aspects of the pollinator's biology.

For ocotillo, which flowers profusely and is self-incompatible, high pollinator density is necessary in order for each of a plant's many flowers to receive or donate outcross pollen. Ocotillo has available to it over much of its range a pollinator on which it can potentially have a large impact, because the reproductive biology of the carpenter bee allows it to capitalize on three to four week flushes of floral resources and its physiology permits it to survive periods of nectar scarcity. However, carpenter bees have rigid nest site requirements. In Texas, acceptable nest plants are abundant at almost all sites where ocotillo occurs, and the population seems to be limited primarily by food. In two of three springs carpenter bees thoroughly harvested the nectar and pollen of ocotillo, and plants had high fruit set and seed set. A flush of floral rewards in summer, provided by other plants, is probably critical to maintaining a high bee density; but ocotillo has a substantial impact on carpenter bee fecundity and population growth. In southern California, the same carpenter bee taxon nests in a palm with a relictual distribution. The bees are therefore unavailable to the majority of ocotillos. The California desert is also more arid than the Big Bend region, and it is possible that lack of floral resources in summer contributes to low bee density there.

Hummingbirds are more flexible than carpenter bees in their nest site requirements, but their lengthy nesting cycle and low clutch size limit the effect that a single plant species can have on population dynamics. Year-round activity and high daily energy requirements mean that a fairly continual supply of nectar is required, not only in the breeding habitat but in other habitats to which a population migrates. A plant depending on hummingbirds for pollination is dependent on many other plant species to help support the bird population. Hummingbird populations are regulated during the period of the year when they encounter the lowest nectar levels (Stiles 1979). Given that plant species vary in abundance and nectar production and that hummingbirds have a slow rate of increase, one might expect that hummingbirds would frequently be at low density relative to nectar availability. This occurred in the southern California desert: for at least two weeks each year, the average ocotillo flower contained more than the 24-hr production rate of 1.5 mg sugar. Yet reports of surplus nectar in hummingbird flowers are rare. In other habitats, hummingbird density closely tracks energy production (Montgomerie and Gass 1981) and frequent visitation keeps available nectar well below the 24-hr production level (Kodric-Brown and Brown 1978, Waser 1978, Brown and Kodric-Brown 1979). As argued in Chapter 4, a possible reason for the disparity between nectar production and hummingbird energy demand in California is that ocotillos are long-lived shrubs which accumulate large energy reserves and can flower massively each year without jeopardizing their survival. Competition for pollinator service during occasional periods of high migrant hummingbird density might have led to a level of flower and nectar production that is usually excessive but not detrimental to fitness.

Waser's (1979) hypothesis that timing of flowering in *F. splendens* has evolved to coincide with migrant hummingbird abundance, which is supported by his Arizona data, is also applicable as a working hypothesis in California, but not in Texas. In Texas, there was not a pronounced passage of migrant hummingbirds in spring, and carpenter

bees were the primary pollinators. The flowering period was shorter than in Arizona and just as predictable in timing. I hypothesize that this well-defined flowering period is the result of selection for profuse flowering to attract nesting carpenter bees early in their active season.

Because of their nectar-robbing habit, carpenter bees are not generally thought of as high-quality pollination mutualists. However, several authors have documented or suggested that carpenter bees are important pollinators (Linsley et al. 1966, Henrickson 1972, Schremmer 1972, Schaffer and Schaffer 1977, Simpson, Neff, and Moldenke 1977b, Waser 1979, Spira 1980, Frankie et al. 1983, Louw and Nicolson 1983). This study revealed that nesting female carpenter bees, in particular, have traits that make them excellent pollinators of adapted flowers: a large requirement for pollen and nectar, lack of territoriality, long foraging bouts, frequent movement between plants, and strong contact with anthers and stigmas. Repeated cutting of flower tubes did not adversely affect seed set; on the contrary, mean seed set increased with the number of cuts.

When the flowers and inflorescences of *F. splendens* are compared with those of two congeners common in the southern Sonoran Desert (Henrickson 1972), it becomes evident that *splendens* is not as specialized as it might be for hummingbird pollination. *Fouquieria macdougalii* and *F. diguetii* appear more specialized for hummingbird pollination and lack the features of *splendens* that facilitate access of carpenter bees to nectar. Their inflorescences are more open, requiring flight from flower to flower. Flowers have slender pedicels and would probably droop under the weight of a large bee. Flower tubes are at least 8 mm longer than in Texas populations of *splendens* and are slightly narrower. Corolla lobes extend the tubular shape of the corolla, instead of being rolled back as in *splendens*. In *macdougalii* and *diguetii*, stigmas are positioned a few mm distal to anthers, a common feature of hummingbird flowers, making it likely that the bird's bill or facial feathers will contact stigmas prior to anthers. In *splendens*, styles

are shorter than filaments, and are often reflexed outward. This may put stigmas in an advantageous position to receive pollen from a carpenter bee when it grasps the flower tube. Other features that distinguish *splendens* and suggest adaptation to carpenter bees are compact flower clusters, stout pedicels, a relatively broad floral tube, and exsertion of stamens well beyond the floral tube.

Traits facilitating pollination by carpenter bees were probably essential to the establishment of *F. splendens* throughout the Chihuahuan Desert, where hummingbirds are scarce in desert scrub. The one trait of *F. splendens* which is anomalous for a hypothesis of adaptation to carpenter bees is the color of the corolla, which is reddish-orange to human vision. In honeybees, color sensitivity declines abruptly beyond the green-yellow portion of the spectrum (from a peak at 530 nm) but extends to 650 nm, slightly into the red (Autrum 1968, Pleasants and Waser 1985). One hypothesis for the prevalence of red color in flowers pollinated by hummingbirds, which have wide spectral sensitivity, is that red is the color "least likely to attract competing Hymenoptera" (Goldsmith and Goldsmith 1979). Most populations of *F. splendens* in the Chihuahuan Desert and all in the Sonoran Desert are reddish-orange; some in Durango and San Luis Potosi are purple-pink, yellow-pink, or white (Henrickson 1972). An analysis of wavelength reflectance by ocotillo flowers has not been made, nor has carpenter bee sensitivity been measured. Stiles (1976) found that certain "orange" and "red" hummingbird flowers (*Diplacus longiflorus* ; *Galvezia speciosa, Ribes speciosum*) reflected strongly beginning at 550 nm and 600 nm, respectively, which is within the range of honeybee sensitivity. Because the flowers have no odor, and because bees investigate budding inflorescences even before flowers open, something about the inflorescence must be visually impressive. Even if the corollas are black to the bee, the inflorescence might stand out against a clear sky. At present, it cannot be argued that a reddish-orange color is more or less effective as an advertisement to carpenter bees than any other color would be.

Bibliography

Addicott, J. F. 1986. On the population consequences of mutualism. Pp. 425-436 *in* J. Diamond and T. J. Case, editors. Community ecology. Harper and Row, New York, New York.

Armbruster, W. S. 1985. Patterns of character divergence and the evolution of reproductive ecotypes of *Dalechampia scandens* (Euphorbiaceae). Evolution 39: 733-752.

Autrum, H. 1968. Color vision in man and animals. Naturwissenschaften 55: 10-18.

Bawa, K. S. 1974. Breeding systems of tree species in a tropical lowland community. Evolution 28: 85-92.

Boinski, S. and P. E. Scott 1988. Association of birds with monkeys in Costa Rica. Biotropica 20: 136-143.

Bolten, A. B., P. Feinsinger, H. G. Baker, and I. Baker. 1979. On the calculation of sugar concentration in flower nectar. Oecologia (Berlin) 41: 301-304.

Brown, J. H. and A. Kodric-Brown. 1979. Convergence, competition, and mimicry in a temperate community of hummingbird-pollinated flowers. Ecology 60: 1022-1035.

Brown, J. H., A. Kodric-Brown, T. G. Whitham, and H. W. Bond. 1981. Competition between hummingbirds and insects for the nectar of two species of shrubs. Southwestern Naturalist 26: 133-145.

Bullock, S. H. 1985. Breeding systems in the flora of a tropical deciduous forest in Mexico. Biotropica 17: 287-301.

Calder, W. A., III, N. M. Waser, S. M. Hiebert, D. W. Inouye, and S. Miller. 1983. Site fidelity, longevity, and population dynamics of Broad-tailed Hummingbirds: a ten year study. Oecologia (Berlin) 56: 359-364.

Carpenter, F. L., D. C. Paton, and M. A. Hixon. 1983. Weight gain and adjustment of feeding territory size in migrant hummingbirds. Proceedings of the National Academy of Sciences USA 80: 7259-7263.

Chappell, M. A. 1982. Temperature regulation of carpenter bees (*Xylocopa californica*) foraging in the Colorado Desert of southern California. Physiological Zoology 55: 267-280.

Cody, M. L. 1968. Interspecific territoriality among hummingbird species. Condor 70: 270-271.

Daniel, T. F. 1984. The Acanthaceae of the southwestern United States. Desert Plants 5: 162-179.

Feinsinger, P. 1983. Coevolution and pollination. Pp. 282-310 *in* D. J. Futuyma and M. Slatkin, eds. Coevolution. Sinauer Associates, Sunderland, Massachusetts.

Frankie, G. W., W. A. Haber, P. A. Opler, and K. S. Bawa. 1983. Characteristics and organization of the large bee pollination system in the Costa Rican dry forest. Pp. 411-447 *in* C. E Jones and R. J. Little, eds. Handbook of experimental pollination ecology. Van Nostrand Reinhold, New York, New York.

Freeman, C. E., W. H. Reid, J. E. Becvar, and R. Scogin. 1984. Similarity and apparent convergence in the nectar-sugar composition of some hummingbird-pollinated flowers. Botanical Gazette 145: 132-135.

Futuyma, D. J. and M. Slatkin. 1983. Introduction. Pp. 1-13 *in* D. J. Futuyma and M. Slatkin, eds. Coevolution. Sinauer Associates, Sunderland, Massachusetts.

Galen, C. 1985. Regulation of seed-set in *Polemonium viscosum*: floral scents, pollination, and resources. Ecology 66: 792-797.

Garrett, K. and J. Dunn. 1981. Birds of southern California: status and distribution. Los Angeles Audubon Society, Los Angeles, California.

Gass, C. L., G. Angehr, and J. Centa. 1976. Regulation of food supply by feeding territoriality in the rufous hummingbird. Canadian Journal of Zoology 54: 2046-2054.

Gass, C. L. and R. D. Montgomerie. 1981. Hummingbird foraging behavior: decision-making and energy regulation. Pp. 159-194 *in* A. C. Kamil and T. S. Sargent, eds. Foraging behavior: ecological, ethological, and psychological approaches. Garland STPM Press, New York, New York.

Geber, M. A. 1985. The relationship of plant size to self-pollination in *Mertensia ciliata*. Ecology 66: 762-772.

Gerling, D. and R. Hermann. 1978. Biology and nesting behavior of *Xylocopa virginica* L. (Hymenoptera, Anthophoridae). Behavioral Ecology and Sociobiology 9: 99-111.

Gilbert, L. E. 1977. The role of insect-plant coevolution in the organization of ecosystems. Pp. 399-413 *in* V. Labeyrie, ed. Comportement des insectes et milieu trophique. Colloques internationeaux 265. Editions du Centre national de la recherche scientifique, Paris.

Goldberg, D. E. and R. M. Turner. 1986. Vegetation change and plant demography in permanent plots in the Sonoran Desert. Ecology 67: 695-712.

Goldsmith, T. H. and K. M. Goldsmith. 1979. Discrimination of colors by the Black-chinned hummingbird, *Archilochus alexandri*. Journal of Comparative Physiology 130: 209-220.

Gottlieb, L. D. 1984. Genetics and morphological evolution in plants. American Naturalist 123: 681-709.

Grant, V. 1958. Regulation of recombination in plants. Cold Spring Harbor Symposium in Quantitative Biology 23: 337-363.

Grant, K. A., and V. Grant. 1968. Hummingbirds and their flowers. Columbia University Press, New York.

Hainsworth, F. R. and L. L. Wolf. 1970. Regulation of oxygen consumption and body temperature during torpor in a hummingbird, *Eulampis jugularis*. Science 168: 368-369.

Henrickson, J. 1972. A taxonomic revision of the Fouquieriaceae. Aliso 7: 439-537.

Henrickson, J. and M. C. Johnston. 1986. Vegetation and community types in the Chihuahuan Desert. Pp. 20-39 *in* J. C. Barlow, A. M. Powell, and B. N. Timmermann, editors. Second symposium on resources of the Chihuahuan Desert region. Chihuahuan Desert Research Institute, Alpine, Texas.

Hurd, P. D., Jr. 1955. The carpenter bees of California. Bulletin of the California Insect Survey 4: 35-72.

Hurd, P. D., Jr. and E. G. Linsley. 1975. The principal *Larrea* bees of the southwestern United States (Hymenoptera: Apoidea). Smithsonian Contributions to Zoology 369.

Hurd, P. D., Jr. and J. S. Moure. 1963. A classification of the large carpenter bees (Xylocopini). University of California Publications in Entomology 29: 1-365.

Kemp, P. R. 1983. Phenological patterns of Chihuahuan Desert plants in relation to the timing of water availability. Journal of Ecology 71: 427-436.

Kodric-Brown, A. and J. H. Brown. 1978. Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant Rufous Hummingbirds. Ecology 59: 285-296.

Krombein, K. V., P. D. Hurd, Jr., D. R. Smith, and B. D. Burks. 1979. Catalog of Hymenoptera in America north of Mexico. Volume 2. Smithsonian Institution Press, Washington, D. C.

Kuban, J. F., Jr. 1977. The ecological organization of hummingbirds in the Chisos Mountains, Big Bend National Park, Texas. M. A. Thesis, University of Texas at Arlington.

Lertzman, K. P. and C. L. Gass. 1983. Alternative models of pollen transfer. Pp. 474-489 *in* C. E Jones and R. J. Little, eds. Handbook of experimental pollination ecology. Van Nostrand Reinhold, New York, New York.

Linsley, E. G., C. M. Rick, and S. G. Stephens. 1966. Observations on the floral relationships of the Galapagos carpenter bee. Pan-Pacific Entomologist 42: 1-18.

Louw, G. N. and S. W. Nicolson. 1983. Thermal, energetic and nutritional considerations in the foraging and reproduction of the carpenter bee *Xylocopa capitata*. Journal of the Entomological Society of Southern Africa 46: 227-240.

McDade, L. A. 1985. Breeding systems of Central American *Aphelandra* (Acanthaceae). American Journal of Botany 72: 1515-1521.

McDade, L. A. and S. Kinsman. 1980. The impact of floral parasitism in two neotropical hummingbird-pollinated plant species. Evolution 34: 944-958.

Moldenke, A. R. 1979. Host-plant coevolution and the diversity of bees in relation to the flora of North America. Phytologia 43: 357-419.

Montgomerie, R. D. 1979. The energetics of foraging and competition in some Mexican hummingbirds. Ph. D. Thesis, McGill University.

Montgomerie, R. D. 1984. Nectar extraction by hummingbirds: response to different floral characters. Oecologia (Berlin) 63: 229-236.

Montgomerie, R. D. and C. L. Gass. 1981. Energy limitation of hummingbird populations in tropical and temperate communities. Oecologia (Berlin) 50: 162-165.

Motten, A. F., D. R. Campbell, D. E. Alexander, and H. L. Miller. 1981. Pollination effectiveness of specialist and generalist visitors to a North Carolina population of *Claytonia virginica*. Ecology 62: 1278-1287.

O'Brien, L. B. and C. W. O'Brien . 1966. Observations on territoriality and a new nesting substrate of *Xylocopa californica arizonensis* Cresson. Pan-Pacific Entomologist 42: 27-29.

Paige, K. N. and T. G. Whitham. 1985. Individual and population shifts in flower color by scarlet gilia: a mechanism for pollinator tracking. Science 227: 315-317.

Phillips, A. R., J. T. Marshall, Jr., and G. Monson. 1964. The birds of Arizona. University of Arizona Press, Tucson.

Pleasants, J. M. and N. M. Waser. 1985. Bumblebee foraging at a "hummingbird" flower: reward economics and floral choice. American Midland Naturalist 114: 283-291.

Powell, A. M. 1988. Trees and shrubs of trans-Pecos Texas. Big Bend Natural History Association, Big Bend National Park, Texas.

Price, M. V. and N. M. Waser. 1979. Pollen dispersal and optimal outcrossing in *Delphinium nelsoni.* Nature 277: 294-296.

Price, M. V. and N. M. Waser. 1984. Experimental studies of pollen carryover: hummingbirds and *Ipomopsis aggregata.* Oecologia (Berlin) 54: 353-358.

Pyke, G. H. and N. M. Waser. 1981. The production of dilute nectars by hummingbird and honeyeater flowers. Biotropica 13: 260-270.

Remsen, J. V., Jr., F. G. Stiles, and P. E. Scott. 1986. Frequency of arthropods in stomachs of tropical hummingbirds. Auk 103: 436-441.

Roubik, D. W. 1982. The ecological impact of nectar-robbing bees and pollinating hummingbirds on a tropical shrub. Ecology 63: 354-360.

Schaffer, W. M., D. B. Jensen, D. E. Hobbs, J. Gurevitch, J. R. Todd, and M. V. Schaffer. 1979. Competition, foraging energetics, and the cost of sociality in three species of bees. Ecology 60: 976-987.

Schaffer, W. M. and M. V. Schaffer. 1977. The reproductive biology of Agavaceae: I. pollen and nectar production in four Arizona agaves. Southwestern Naturalist 22: 157-168.

Schmidt, R. H., Jr. 1986. Chihuahuan climate. Pp. 40-63 *in* Barlow, J. C., A. M. Powell, and B. N. Timmermann, eds. Second symposium on resources of the Chihuahuan Desert region. Chihuahuan Desert Research Institute, Alpine, Texas.

Schremmer, F. 1972. Der Stechsaugrussel, der Nektarraub, das Pollensammeln und der Blutenbesuch der Holzbienen (*Xylocopa*) (Hymenoptera, Apidae). Zeitschrift fur Morphologie der Tiere 72: 263-294.

Scott, P. E. 1983. Comparative nesting ecology of Lucifer and Black-chinned Hummingbirds. Abstract, Second Chihuahuan Desert Symposium. Chihuahuan Desert Research Institute, Alpine, Texas.

Shreve, F. 1917. The establishment of desert perennials. Journal of Ecology 5: 210-216.

Simpson, B. B. 1977. Breeding systems of dominant perennial plants of two disjunct warm desert ecosystems. Oecologia (Berlin) 27: 203-226.

Simpson, B. B. and J. L. Neff. 1983. Evolution and diversity of floral rewards. Pp. 142-159 *in* C. E. Jones and R. J. Little, editors. Handbook of experimental pollination biology. Van Nostrand Reinhold, New York, New York.

Simpson, B. B., J. L. Neff, and A. R. Moldenke. 1977a. Reproductive systems of *Larrea*. Pages 92-114 *in* T. J. Mabry, J. H. Hunziker, and D. R. DiFeo, editors. Creosotebush. Biology and chemistry of *Larrea* in New World deserts. Dowden, Hutchinson and Ross, Inc., Stroudsburg, Pennsylvania.

Simpson, B. B., J. L. Neff, and A. R. Moldenke. 1977b. *Prosopis* flowers as a resource. Pages 84-107 *in* B. B. Simpson, ed. Mesquite. Its biology in two desert scrub ecosystems. Dowden, Hutchinson and Ross, Inc., Stroudsburg, Pennsylvania.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry. Second edition. W. H. Freeman, San Francisco, California.

Spira, T. P. 1980. Flower parameters, breeding system and pollinator type in *Trichostema* (Labiatae). American Journal of Botany 67: 278-284.

Steel, R. G. D. and J. H. Torrie. 1980. Principles and procedures of statistics: a biometrical approach. Second edition. McGraw-Hill, New York, New York.

Stiles, F. G. 1973. Food supply and the annual cycle of Anna's Hummingbird. University of California Publications in Zoology 97: 1-109.

Stiles, F. G. 1976. Taste preferences, color preferences, and flower choice in hummingbirds. Condor 78: 10-26.

Stiles, F. G. 1979. El ciclo anual en una comunidad coadaptada de colibries y flores en el bosque tropical muy humedo de Costa Rica. Revista de Biologia Tropical 27: 75-101.

Stiles, F. G. 1981. Geographical aspects of bird-flower coevolution, with particular reference to Central America. Annals of the Missouri Botanical Garden 68: 323-351.

Strickler, K. 1979. Specialization and foraging efficiency of solitary bees. Ecology 60: 998-1009.

Turner, R. M. and D. E. Brown. 1982. Sonoran Desertscrub. Pp. 181-221 *in* D. E. Brown, ed. Biotic communities of the American southwest -- United States and Mexico. Desert Plants 4 (Special Issue).

Tyrell, E. Q. and R. A. Tyrell. 1985. Hummingbirds: their life and behavior. Crown Publishers, New York, New York.

Uyenoyama, M. K. 1987. On the evolution of genetic incompatibility systems: incompatibility as a mechanism for the regulation of outcrossing distance. Pp. 212-232 *in* R. Michod and B. Levin, eds. The evolution of sex. Sinauer Associates, Sunderland, Massachusetts.

Waser, N. M. 1978. Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. Ecology 59: 934-944.

Waser, N. M. 1979. Pollinator availability as a determinant of flowering time in ocotillo (*Fouquieria splendens*). Oecologia (Berlin) 39: 107-121.

Waser, N. M. 1983. The adaptive nature of floral traits: ideas and evidence. Pp. 241-285 *in* L. Real (ed.). Pollination Biology. Academic Press, Orlando, Florida.

Waser, N. M. 1988. Comparative pollen and dye transfer by pollinators of *Delphinium nelsonii*. Functional Ecology 2: 41-48.

Waser, N. M. and M. V. Price. 1981. Pollinator choice and stabilizing selection for flower color in *Delphinium nelsonii*. Evolution 35: 376-390.

Waser, N. M. and M. V. Price. 1982. A comparison of pollen and fluorescent dye carry-over by natural pollinators of *Ipomopsis aggregata*. Ecology 63: 1168-1172.

Waser, N. M. and M. V. Price. 1984. Experimental studies of pollen carryover: effect of floral variability in *Ipomopsis aggregata*. Oecologia (Berlin) 62: 262-268.

Waser, N. M. and L. A. Real. 1981. Effective mutualism between sequentially flowering plant species. Nature 281: 670-672.

Watmough, R. H. 1983. Mortality, sex ratio and fecundity in natural populations of large carpenter bees (*Xylocopa* spp.). Journal of Animal Ecology 52: 111-125.

Wauer, R. H. 1971. Ecological distribution of birds of the Chisos Mountains, Texas. Southwestern Naturalist 16: 1-29.

Wauer, R. H. 1973. Birds of Big Bend National Park and vicinity. University of Texas Press, Austin.

Table 2.1. Wet-season and dry-season rainfall (in mm) at Panther Junction, Big Bend National Park (elevation 1136 m).

	1985-86	1986-87	1987-88	31-year $\bar{x} \pm$ S.D.
May - October	419.1	438.8	329.4	280.3 ± 95.1
November - April	66.1	162.0	35.5	75.2 ± 39.9

Table 2.2. Characteristics of *Fouquieria splendens* study sites in foothills of Chisos Mountains.

Site	Description	Hummingbird and carpenter bee abundance
Rough Spring	1180 m elevation At base of igneous slickrock slope adjacent to wash.	**Hummingbirds:** CL, AA* resident Apr.-Aug. Density of nests often high (up to 15 active simultaneously, see Table 2.4). CL nested on slopes among *Fouquieria splendens*, but fed primarily on *Penstemon havardii*, *Castilleja lanata*, and *Anisacanthus linearis* in wash 0.5-2.0 km N of site. Nearest feeder: 6 km. **Carpenter bees:** common, nesting in DL, AL on rock slopes and grassy flats.
Panther Canyon	1270 m elevation On igneous slickrock slope adjacent to wash	**Hummingbirds:** CL, AA resident Mar.-Aug. Density of nests high (Table 2.4), some females raising 2 broods in succession. Density reflects ideal nesting habitat (for CL, slickrock slopes and suitable nest plants; for AA, wooded washes), nectar plant diversity (especially *P. havardii*, *Agave havardiana*, *A. linearis*), and availability of sugar-water feeders at Panther Junction. Two color-marked CL females commuted 2.5 km from nests to feeders.

		Carpenter bees: common, nesting in AH, AL, DL * on slopes.
Basin	1580 m elevation On grassy-rocky talus slope, lower edge juniper-oak zone.	**Hummingbirds**: 1-2 male CL seen regularly near site; 5 CL nests found on slope 2 km west; AA nests in wooded wash 1 km distant. Nearest feeder: 1 km. **Carpenter bees:** Common, nesting in AH, DL.
Pummel	1140 m elevation Edge of wash, 0.3 km from mountain cliffs and slopes, desert grassland adjacent.	**Hummingbirds**: 2-3 male CL territorial within 1.5 km, along wash, when *P. havardii* in bloom; females seen regularly, AA occasionally; probably 3-5 CL nests within 1 km of site, but none found. Nearest feeder: 5 km. **Carpenter bees:** Common, nesting in DL, YE.
Cattail	1210 m elevation Gravelly slope bordering wash, desert grassland adjacent.	**Hummingbirds**: 1-2 male AA, 1-2 male CL seen regularly; 1 AA nest 0.5 km distant . Nearest feeder: 6 km. **Carpenter bees**: fairly common, nesting in DL

* Abbreviations: CL = *Calothorax lucifer*, AA = *Archilochus alexandri*; AH = *Agave havardiana*, AL = *Agave lechuguilla*, DL = *Dasylirion leiophyllum*, YE = *Yucca elata*.

Table 2.3. Characteristics of *Fouquieria splendens* study sites on outwash plains surrounding Chisos Mountains.

Site	Description	Hummingbird and carpenter bee abundance
Maverick	860 m elevation Level plain above wash; "forest" of ocotillo, open desert scrub	**Hummingbirds**: usually absent; an occasional transient. Nearest feeder: 6 km (Study Butte). **Carpenter bees**: usually rare, not nesting commonly within 5 km; sometimes common after discovering flowers late in season.
Dugout	910 m elevation sloping outwash plain, desert scrub.	**Hummingbirds**: usually 1 AA or CL * seen; 1 AA nest in cottonwood oasis 1 km distant; nearest CL nest probably 3 km. Nearest feeder: 9 km. **Carpenter bees**: common foragers, nesting 2-3 km distant.
KBar	1000 m elevation sloping outwash plain, desert scrub.	**Hummingbirds**: usually absent; an occasional transient. Nearest feeder: 5 km. **Carpenter bees**: common foragers; 1 nest near site in DL; nesting more commonly 2 km distant.

* Abbrevations as in Table 2.2.

Table 2.4. Number of hummingbird nests found within 1 km of *Fouquieria splendens* plots in foothills of Chisos Mountains.

Site	Year	Nest searches [a]	Species [b]	Number of nests initiated				
				April	May	June	July	August
Rough Spring	1986	May: 3, June: 4,	CL	1	0	15	7	
		July: 5	AA	1	1	3		
	1987	April: 1, May: 2,	CL	4	4	2		
		June: 2	AA	1	0	1		
Panther	1985	March: 1, April: 8,	CL	9	7	0	6	1
Canyon		May: 8, June: 7,	AA	13	12	1	0	0
		July: 2, August: 4						

[a] Number of days in which one hour or more was spent searching for nests. Some nests were discovered by chance on other days. In 1986, two observers searched in June and July.

[b] CL = *Calothorax lucifer*, AA = *Archilochus alexandri*

Table 2.5. Nectar accumulation in unbagged, uncut *Fouquieria splendens* flowers on dates when carpenter bees and other nectar consumers were rare or absent. Values are means ± standard errors (n).

		MICROLITERS		MILLIGRAMS
SITE	DATE	NECTAR	CONCENTRATION [a]	SUGAR
Maverick	27 Apr 1987	9.5 ± 0.7 (47)	33.0 ± 1.2 (36)	3.7 ± 0.3 (47)
	5 Apr 1988	4.3 ± 0.4 (30)	78.5 ± 2.2 (24)	4.6 ± 0.5 (30)
	20 Apr 1988	4.9 ± 0.7 (29)	63.1 ± 2.2 (24)	3.8 ± 0.4 (30)
KBar	26 Apr 1987	6.5 ± 0.8 (32)	26.1 ± 1.7 (11)	1.5 ± 0.2 (32)
	1 May 1987	6.0 ± 1.1 (26)	29.7 ± 1.7 (17)	1.5 ± 0.3 (26)
Dugout	30 Apr 1987	3.9 ± 0.7 (19)	21.0 ± 1.2 (20)	1.1 ± 0.2 (19)
	7 May 1987	7.3 ± 0.8 (29)	24.4 ± 1.4 (14)	2.4 ± 0.3 (29)

[a] mass of solutes / mass of solution x 100

Table 2.6. Test of the breeding system of *Fouquieria splendens* and the effectiveness of natural pollinators at Big Bend National Park.

	FLOWERS SETTING FRUIT		SEEDS / FRUIT		SEEDS / FLOWER
TREATMENT [a]	%	(n)	$\bar{x}$ ± S.D. (n)	range	mean
AUTOGAMY [b]	10.0	(462)	1.6 ± 1.4 (42)	1-8	0.15
HAND-SELF [c]	10.0	(300)	1.7 ± 1.2 (29)	1-6	0.16
HAND-OUTCROSS (nearest neighbor)	87.8	(287)	4.3 ± 2.9 (243)	1-13	3.79
HAND-OUTCROSS (1 km)	72.3	(303)	4.0 ± 3.1 (212)	1-13	2.93
NATURAL (accessible to pollinators)	58.4	(385)	3.7 ± 3.0 (225)	1-14	2.16

[a] Treatments were replicated on 6 plants at Maverick, 14-20 April 1987.

[b] Test of ability to self-pollinate; flowers bagged but not hand-pollinated.

[c] Flowers pollinated by hand, using pollen from other flowers on same plant.

Table 2.7. Two-way ANOVA on breeding test data in Table 2.6. Variable is proportion of flowers forming fruits (arc-sine transformed).

SOURCE	DF	SS	F	Pr > F
Plant	5	0.17	0.9	0.5
Treatment	4	4.92	32.6	0.0001
Error	20	0.76		
Treatment Contrasts:				
1. A v. B	1	0.00	0.01	0.9
2. B v. C + D	1	3.08	81.6	0.0001
3. C v. D	1	0.31	8.3	0.01
4. E v. C + D	1	0.47	12.5	0.002

A = AUTOGAMY C = HAND-OUTCROSS (NEAR) E = NATURAL

B = HAND-SELF D = HAND-OUTCROSS (1 KM)

Table 2.8. Two-way factorial ANOVA on breeding test data in Table 2.6. Variable is the number of seeds per fruit.

SOURCE	DF	SS	F	Pr > F
Plant	5	507.1	13.1	0.0001
Treatment	4	290.2	9.4	0.0001
Plant x Treatment	20	232.5	1.5	0.07
Error	721	5590.9		
Treatment Contrasts:				
1. A v. B	1	4.0	0.5	0.48
2. B v. C + D	1	86.4	11.1	0.0009
3. C v. D	1	1.6	0.2	0.65
4. E v. C + D	1	13.6	1.8	0.19

A = AUTOGAMY C = HAND-OUTCROSS (NEAR) E = NATURAL

B = HAND-SELF D = HAND-OUTCROSS (1 KM)

Table 2.9. Visitation by hummingbirds and carpenter bees, and availability of nectar and pollen in ocotillo flowers in 1986, 1987, and 1988.

					AVAILABILITY AT MIDDAY		
			HUMMINGBIRD[c]	CARPENTER BEE	NECTAR[d]		POLLEN[e]
Site	Habitat[a]	Date[b]	visits/ inflor. x hr	cuts/flower[d]	microliters	mg sugar	% remaining
		1986:					
Dugout	D	1	0.01	--	--		--
		2	0.00	3.4 ± 0.27	0.16 ± 0.08		69
K-Bar	D	1	0.03	--	--		--
		2	0.00	4.8 ± 0.19	0.00		0
Maverick	D	1	0.00	--	--		--
		2	0.01	4.1 ± 0.24	0.02 ± 0.01		34
Rough Spr.	F	1	0.00	--	--		--
		2	0.00	3.6 ± 0.20	0.01		20
Panther	F	1	0.05	--	--		--
		2	0.09	--	--		--
Basin	F	1	0.01	--	--		--
		2	0.02	4.2 ± 0.20	0.00		2

		1987:	(humm. visits)	(cuts/flower)	(ul nectar)	(mg sugar)	(pollen, %)
Dugout	D	1	0.00	0.4 ± 0.08	6.07 ± 0.61	1.44 ± 0.15	53
		2	0.00	0.7 ± 0.12	4.79 ± 0.72	1.27 ± 0.18	4
K-Bar	D	1	0.00	1.0 ± 0.13	2.98 ± 0.37	0.82 ± 0.10	0
		2	0.00	0.6 ± 0.11	6.77 ± 0.52	2.32 ± 0.19	30
Maverick	D	1	0.00	0.1 ± 0.05	9.17 ± 0.70	3.53 ± 0.32	75
		2	0.00	0.9 ± 0.14	1.46 ± 0.32	0.53 ± 0.11	36
		1988:					
Dugout	D	1	0.00	1.9 ± 0.24	0.17 ± 0.07	0.16 ± 0.06	62
		2	0.00	2.8 ± 0.19	0.20 ± 0.05	0.09 ± 0.03	30
K-Bar	D	1	0.00	2.8 ± 0.27	0.24 ± 0.05	0.12 ± 0.03	33
		2	0.00	3.8 ± 0.28	0.33 ± 0.10	0.15 ± 0.05	0
Maverick	D	1	0.00	0.0	4.25 ± 0.41	4.64 ± 0.49	100
		2	0.00	0.03 ± 0.03	4.90 ± 0.67	3.76 ± 0.38	100
Rough Spr.	F	1	0.00	2.6 ± 0.23	0.27 ± 0.04	0.13 ± 0.02	42
		2	0.09	3.5 ± 0.33	0.31 ± 0.06	0.08 ± 0.02	20
Pummel	F	1	0.09	2.9 ± 0.25	0.12 ± 0.06	0.10 ± 0.06	69
		2	0.00	2.3 ± 0.24	0.24 ± 0.05	0.08 ± 0.02	13
Cattail	F	1	0.24	3.4 ± 0.31	0.03 ± 0.01	0.02 ± 0.01	45
		2	0.19	1.2 ± 0.23	0.31 ± 0.07	0.19 ± 0.04	27

[a] D = desert (open desert scrub on outwash plains); F = foothills of Chisos Mountains.

[b] Dates were at least 5 days apart.

[c] *Calothorax lucifer* and *Archilochus alexandri*

[d] Values are mean ± 1 standard error (n = 50 flowers in 1986 and 1987; n = 30 in 1988). In 1986 flowers were not sampled on some dates.

[e] % of flowers with pollen remaining on anthers (n as in footnote d).

Table 2.10. Infrequent or irregular visitors to *Fouquieria splendens* flowers. Data in year columns are number of observation periods during which a species was recorded and its visitation frequency (c = common, u = uncommon, r = rare). A visitor was "common" if an average flower received > 1 visit/day and "rare" if < 5% of flowers were visited.

			YEAR (no. observation periods)		
Visitor	Reward	Potential pollinator [a]	1986 (12)	1987 (6)	1988 (12)
Scott's Oriole	nectar	+	1u, 1r	1u, 1r	2u, 2r
Verdin	nectar	-	2r	0	1u, 2r
Bombus sonorus	nectar	+	1c, 2u, 2r	1r	1c, 5u
Apis mellifera	nectar	-	2c, 3u, 4r	1c	1c
large anthophorid bee	nectar	+	1u, 1r	1u	1r
halictid sp. "A"	pollen	+	1r	3c	1r
halictid sp. "B"	pollen	+	2r	3c, 1u	2r
beefly (*Anthrax xylocopae*)	nectar	+	2r	1c	0
Lepidoptera [b]	nectar	+	1u, 3r	0	0
wasp	?	-	2c, 4u, 2r	0	1c,1u

[a] contacted anthers and probably stigmas with some regularity.

[b] *Battus* sp., 2 unidentified butterfly species, and 1 unidentified skipper.

Table 2.11. Nested analysis of variance on a measure of carpenter bee visitation rate to ocotillo flowers: cuts/flower (data in Table 2.9).

Source of variation	df	Mean Square	Variance component	% of total	Expected Mean Squares
Among years	2	793.4	2.56	52.5	$\sigma_E^2 + 43.4\,\sigma_{D(S)}^2 + 69.2\,\sigma_{S(H)}^2 + 199.9\,\sigma_{H(Y)}^2 + 296.8\,\sigma_Y^2$
Habitats within years	2	27.9	- 0.09	0	$\sigma_E^2 + 39.4\,\sigma_{D(S)}^2 + 54.6\,\sigma_{S(H)}^2 + 149.1\,\sigma_{H(Y)}^2$
Sites within habitats	9	47.4	0.47	9.7	$\sigma_E^2 + 40.4\,\sigma_{D(S)}^2 + 65.1\,\sigma_{S(H)}^2$
Dates within sites	9	15.3	0.37	7.6	$\sigma_E^2 + 36.9\,\sigma_{D(S)}^2$
Error (within dates)	881	1.5	1.48	30.2	σ_E^2
Total	903		4.89	100.0	

Table 2.12. Fruit set and seed set of naturally pollinated ocotillo flowers in two habitats, Texas 1986-1988.

Year	Site	Habitat [a]	% Fruit Set $\bar{x} \pm$ S.E. (inflor.'s)	Seeds / Fruit $\bar{x} \pm$ S.E. (fruits)
1986	Dugout	D		8.4 ± 0.2 (100)
	KBar	D		10.0 ± 0.4 (60)
	Maverick	D		9.5 ± 0.3 (100)
	Rough Spr.	F		10.3 ± 0.2 (200)
	Panther	F		8.0 ± 0.4 (91)
	Basin	F		8.3 ± 0.2 (200)
1987	Dugout	D	55.2 ± 4.2 (11)	4.4 ± 0.2 (219)
	KBar	D	44.6 ± 4.2 (11)	3.9 ± 0.1 (411)
	Maverick	D	58.9 ± 4.9 (6)	3.7 ± 0.2 (225)
1988	Dugout	D	82.0 ± 1.0 (498)	8.3 ± 0.2 (200)
	KBar	D	81.4 ± 1.3 (249)	8.6 ± 0.1 (200)
	Maverick	D	17.9 ± 0.7 (435)	2.0 ± 0.1 (200)
	Rough Spr.	F		7.9 ± 0.2 (200)
	Pummel	F		7.6 ± 0.2 (200)
	Cattail	F		7.2 ± 0.2 (200)

[a] D = Desert (outwash plains), F = Foothills

Table 2.13. Effect of hand-outcrossing ocotillo flowers at Maverick on 6 April 1988, during period of pollinator scarcity.

Inflorescence Treatment	% Fruit Set (n)	Seeds/Fruit mean ± S.E.	Seeds/Flower
Flowers accessible to pollinators, but pollinators rare or absent; flowers hand-pollinated once with pollen from *two neighbors*	84.1 (138)	6.5 ± 0.84 (116)	5.4
Flowers accessible to pollinators (control for treatment above)	14.5 (193)	1.5 ± 0.19 (26)	0.2

Table 2.14. Visits by carpenter bees to single ocotillo plants and average reward levels at various sites in 1988. Each plant was observed for 2 hours in early or mid-morning except for the experimental plant * observed on 27 April from 3:00 to 5:00 pm. Its inflorescences were bagged for 24 hours to increase the initial amount of nectar and pollen available.

Date:	9 Apr	21 Apr	22 Apr	24 Apr	25 Apr	27 Apr *
No. open flowers:	274	251	129	87	199	159
Carpenter bees:						
Visits/plant x hr: [a]	12.7	10.0	15.0	12.5	8.0	13.5
Visits/flower x hr: [a]	0.35	0.42	0.95	0.80	0.17	1.48
Flowers/visit						
(Female bees):	12.3	11.5	11.1	6.0	4.2	19.6
$\bar{x} \pm$ S.D. (n)	$\pm$ 10.9	$\pm$ 14.9	$\pm$ 12.9	$\pm$ 3.7	$\pm$ 3.2	$\pm$ 20.0
	(13)	(16)	(19)	(21)	(13)	(22)
Bumblebee queens:						
Visits/flower x hr:	0.01	0.12	0.00	0.00	0.49	0.00
Microliters nectar						
($\bar{x}$) before/after : [b]	1.7 / 0.5	1.2 / 0.2	0.5 / 0.2	0.7 / 0.2	0.9 / 0.3	2.5 / 0.3

Pollen: % remaining						
before / after : [b]	26 / 20	43 / 1	no data	55 / 44	34 / 32	51 / 19

[a] includes visits by male and female bees.

[b] based on samples of 30 flowers. Values for nectar are means. Values for pollen are the percentages of flowers with some pollen remaining on anthers.

Table 2.15. Some examples of partial foraging bouts by female carpenter bees visiting ocotillo plants at KBar, 26 April 1988. Observations began when a foraging bee entered a new plant and continued until it left the patch or was lost. AM = between 8:00 and 10:00; PM = between 5:00 and 7:00.

	DURATION															
TIME	min: seconds	FLOWERS VISITED / PLANT														
AM	4:17	7	1	2	1	2	2	7	8	1	4	1				
AM	6:27	5	2	11	8	11	14	4	2	1						
AM	7:01	6	2	4	5	74										
AM	(not timed)	8	3	2	13	11	1	9	3	5	6	8	1	4	4	10
PM	4:14	2	18	19	5	1	2	1	5							
PM	5:00	1	1	22	22	8	1	2								
PM	8:20	2	1	28	7	2	10	28	31							
PM	9:00	3	11	1	16	1	2	25	6	4	5	2	8	2	7	15

Table 2.16. Timing of flower opening in ocotillo.

Site: Dugout[a]

Time interval:	6 pm - noon	noon - 6 pm
no. opened (%)	54 (38%)	88 (62%)

Site: Basin[b]

Time interval:	6 pm - 8 am	8 - 11 am	11 am - 2 pm	2 - 6 pm
no. opened (%)	23 (27%)	9 (10%)	27 (31%)	27 (31%)

---

a 1-3 April 1986. Sums for 10 inflorescences, 2/plant.

b 25-26 April 1986. Sums for 16 inflorescences, 1/plant.

Table 2.17. Corolla tube length in samples of *Fouquieria splendens* flowers from Big Bend National Park, Texas, and Anza-Borrego Desert State Park, California.

Site	Year	Mean ± S. D.	N	No. sampling dates
TEXAS:				
Basin	1986	14.1 ± 1.3	49	1
Boquillas	1987	14.4 ± 1.4	57	1
Cattail	1988	13.6 ± 1.3	27	1
Dugout	1987	14.3 ± 1.5	94	2
KBar	1987	13.2 ± 1.3	100	2
Maverick	1987	14.7 ± 1.8	86	2
	1988	15.2 ± 1.3	49	1
Pummel	1988	13.9 ± 0.8	29	1
Rough Spring	1986	13.3 ± 1.0	26	1
CALIFORNIA:				
Bow Willow	1987	20.5 ± 2.1	74	2
	1988	20.3 ± 1.8	74	3
Desert Gardens	1987	21.5 ± 1.8	68	3
	1988	20.0 ± 1.8	77	2
Mountain Palm Springs	1988	18.6 ± 1.7	26	1

Table 3.1. Important pollen and nectar sources of carpenter bees (*Xylocopa californica arizonensis)* in Big Bend National Park.

			MONTHS OF USAGE[c]			
SPECIES	Growth Form [a]	Resource Obtained [b]	1985	1986	1987	1988
Larrea tridentata	S	P, N	7	4 67		4
Guaiacum angusifolium	S	N			45	45
Prosopis glandulosa	T	P (N?)	4			4
Fouquieria splendens	S	P, N*	45	4	45	45
Penstemon havardii	H	N*	456	45	56	
Chilopsis linearis	T	N*		56		5
Agave lechuguilla	R	P, N	5	5 78	6	
Agave havardiana	R	N		56		
Dasylirion leiophyllum	R	?		67	5	
Aloysia gratissima	S	?	7	6 9	56	
Tecoma stans	S	N*	7	67		
Maurandya antirrhiniflora	V	N*	8	7		

Anisacanthus linearis	S	N*	678	89		
Months of observation[c]:			45678	456789	456	45

---

[a] H = herbaceous perennial; R = shrub with a rosette of succulent leaves; S = shrub; T = tree; V = vine.

[b] N = nectar; N* = nectar taken by piercing base of corolla, usually without contacting anthers or stigmas, except in *Fouquieria splendens*; P = pollen gathered deliberately by female bee.

[c] 4 = April, 5 = May, etc. Underlining a month signifies that female *X. californica* were seen gathering pollen from that species in that month. Records are based mainly on casual observations of foraging bees.

Table 3.2. Percentages ($\bar{x} \pm$ S.D.) of pollen taxa, by grains and by volume, in samples from 16 carpenter bee nests.

CATEGORY	*Fouquieria splendens*	*Prosopis glandulosa*	Zygophyllaceae	Other taxa
GRAINS	52.9 ± 25.7	38.7 ± 25.7	7.7 ± 13.6	0.8 ± 1.2
VOLUME	68.9 ± 22.6	29.1 ± 22.1	2.0 ± 4.0	---

Table 4.1. Flowering phenology of *Fouquieria splendens* at 4 sites in Anza-Borrego Desert State Park, California, in 1987, based on censuses of 20 permanently marked plants at each site.

Site	Date	Mean no. Inflorescences per plant in Bud	in Flower	Finished
Bow Willow	28 February	18.9	3.2	12.9
	9 March	30.3	7.0	16.6
	16 March	no data	4.0	no data
	30 March	35.1	5.3	no data
Desert Gardens	10 March	89.8	5.1	2.5
	17 March	no data	6.1	no data
	27 March	no data	10.3	no data
Glorietta Canyon	7 March	19.2	0.2	4.2
	22 March	24.1	0.2	no data
Mescal Bajada	4 March	11.8	5.2	1.7
	12 March	21.8	9.1	2.9
	22 March	22.5	7.6	8.0
	29 March	31.3	9.1	3.4

Table 4.2. Flowering phenology of *Fouquieria splendens* at 4 sites in Anza-Borrego Desert State Park, California, in 1988, based on censuses of 20 permanently marked plants at each site.

Site	Date	Mean no. Inflorescences per plant in Bud	in Flower	Finished
Bow Willow	4 March	65.9	3.7	0.0
	13 March	72.7	8.4	0.1
	20 March	54.0	18.1	0.7
	14 April	0.4	4.8	79.9
Desert Gardens	7 March	88.4	1.6	0.4
	17 March	no data	6.6	no data
	16 April	0.8	10.7	99.9
Glorietta Canyon	20 March	28.9	6.1	0.1
	16 April	0.4	8.7	33.9
Mescal Bajada	5 March	40.1	1.8	0.0
	21 March	52.4	3.7	0.2
	17 April	2.0	29.0	31.1

Table 4.3. Visitation by hummingbirds, orioles, and carpenter bees, and available nectar in ocotillo flowers: California, 1987.

	Hummingbird [a]		Nectar (means) [b]		% of flowers cut by [b]		
1987	visits/inflor. x hr	species	microliters	mg sugar	orioles	carp. bees	Site [c]
Mar 3	0.00	--	14.4	3.5	0	2	B
5	0.00	--	8.4	3.6	0	0	M
9	0.03	c	4.2	1.0	30	22	B
12	0.00	--	6.3	2.6	0	5	M
17	0.13	c	4.6	1.5	25	0	D
18	0.11	c, a	5.1	1.6	43	0	D
20	0.14	r	1.5	0.6	11	10	D
21	0.34	r	0.9	0.4	40	0	D
23	0.28	r	0.5	0.3	46	8	D
26	0.52	r	0.7	0.4	42	0	D
27	0.03	r	2.8	2.5	8	0	D
28	0.01	u	5.7	3.3	14	2	M

[a] Patches of 2-5 plants were observed for 2 hours. Hummingbird species were Allen's (a), Costa's (c), Rufous (r), and unidentified (u).

[b] Based on samples of 20-50 flowers collected after observations.

[c] B = Bow Willow, D = Desert Gardens, M = Mescal Bajada.

Table 4.4. Nectar production in ocotillo flowers: Mescal Bajada, California, 23-24 March 1987.

	24-hr accumulation $\bar{x} \pm$ S.E. (n)	Standing crop before bagging $\bar{x} \pm$ S.E. (n)
Microliters	6.7 ± 0.68 (60)	2.5 ± 0.59 (54)
Milligrams sugar	2.1 ± 0.16 (60)	0.6 ± 0.12 (54)
Concentration [a]	29.5 ± 1.55 (38)	24.2 ± 2.86 (11)

[a] mass solutes / mass solution x 100

Table 4.5. Nesting activity by Costa's Hummingbird in Anza-Borrego Desert State Park, California. Observations were made between 28 February and 30 March 1987, 3 and 23 March 1988, and 14 and 17 April 1988. Abbreviations: FS = *Fouquieria splendens*, JC = *Justicia californica*.

Site of nest or other record	Date and observation
Glorietta Canyon: nest on unidentified shrub in wash with abundant flowering JC.	8 March 1987: 2 eggs. No further data.
Glorietta Canyon: nest on jojoba bush in same wash.	8 March 1987: 1 egg. No further data.
Mescal Bajada: nest on unidentified shrub in wash with abundant flowering JC; flowering FS nearby.	29 March 1987: 2 young ca. 5 days post-hatch. No further data.
Throughout park	30 March 1987: no fledgling Costa's yet seen.
Near Tamarisk Grove [a]: nest on FS branch on slope among flowering JC and FS.	16 March 1988: 2 eggs. 14 April: 2 young near fledge. 16 April: young gone from nest.

Mountain Palm Springs: nest on indigo bush on slope among flowering FS	22 March 1988: 2 hatchlings. 14 April: 2 fledglings perched 15 m from nest, fed by adult female; female also sitting at intervals on a new egg in her old nest. 15 April: still 1 egg in nest; female sitting at intervals and feeding fledglings. Adult and fledglings visit FS flowers, the principal nectar source but near the end of flowering. Egg collected for use in nutritional study.[b] 16 April: nest empty; female continues to feed fledglings, does not visit nest.
Bow Willow: in a stand of FS.	14 April 1988: one fledgling visits FS flowers.

[a] Found by Paul Reddish.

[b] Collected under State of California permit # 2092 to Ann Brice, University of California (Davis).

Table 4.6. Characteristics of Rufous Hummingbird territories among ocotillos at Desert Gardens, California: 1987.

DATE	SEX	PLANTS DEFENDED	TOTAL FLOWERS	TOTAL SUGAR [a]
21 March	M	10	1,771	2.66 g
23 March	M	3	1,668	2.50 g
26 March	F	3	1,378	2.07 g

[a] Assuming 1.5 mg sugar / flower x day.

Table 4.7. Visitation by hummingbirds, orioles, and carpenter bees, and available nectar and pollen in ocotillo flowers: California, 1988. Hummingbird visit rate was based on 2-hr observation periods, other data on samples of 30 or 40 flowers (5/plant).

	Hummingbird [a]		Nectar (means)		Pollen: %	% of flowers cut by		
1988	visits/inflor x hr	species	microliters	mg sugar	remaining [b]	orioles	carp. bees	Site [a]
Mar 6	0.00	--	12.0	4.3	100	0	0	B
10	0.03	r	8.4	5.0	98	0	0	D
12 [c]	--	--	--	--	--	0	77	P1
13	0.00	--	9.6	5.6	83	0	0	B
19 [c]	--	--	--	--	--	--	65	P1
19	0.00	--	6.0	4.0	97	0	3	P2
20	0.00	--	13.7	6.3	100	0	3	B
21	0.00	--	6.8	5.9	100	0	0	D

[a] Abbreviations as in Table 4.1, except sites P1 and P2. which were each near a different grove of palms (2 km apart) at Mountain Palm Springs.

[b] % of flowers with pollen remaining on anthers.

[c] Visit rate not measured, flowers checked only for carpenter bee cuts.

Table 4.8. Fruit set of ocotillo flowers opening between 1 and 16 March 1987 at California sites (abbreviations as in Table 4.3).

Site	Plant	No. flowers	No. fruits developing (30 March)	% Fruit set
B	1	79	0	0.0
	2	303	2	0.7
	3	345	5	1.4
	4	118	14	11.9
	5	268	36	13.4
M	1	153	0	0.0
	2	186	0	0.0
	3	323	0	0.0
	4	116	0	0.0
	5	105	0	0.0

Table 4.9. Fruit set and seed set of ocotillo flowers opening between 6 and 18 March 1988 at Bow Willow, California. See also Table 4.10, "accessible to pollinators" treatment.

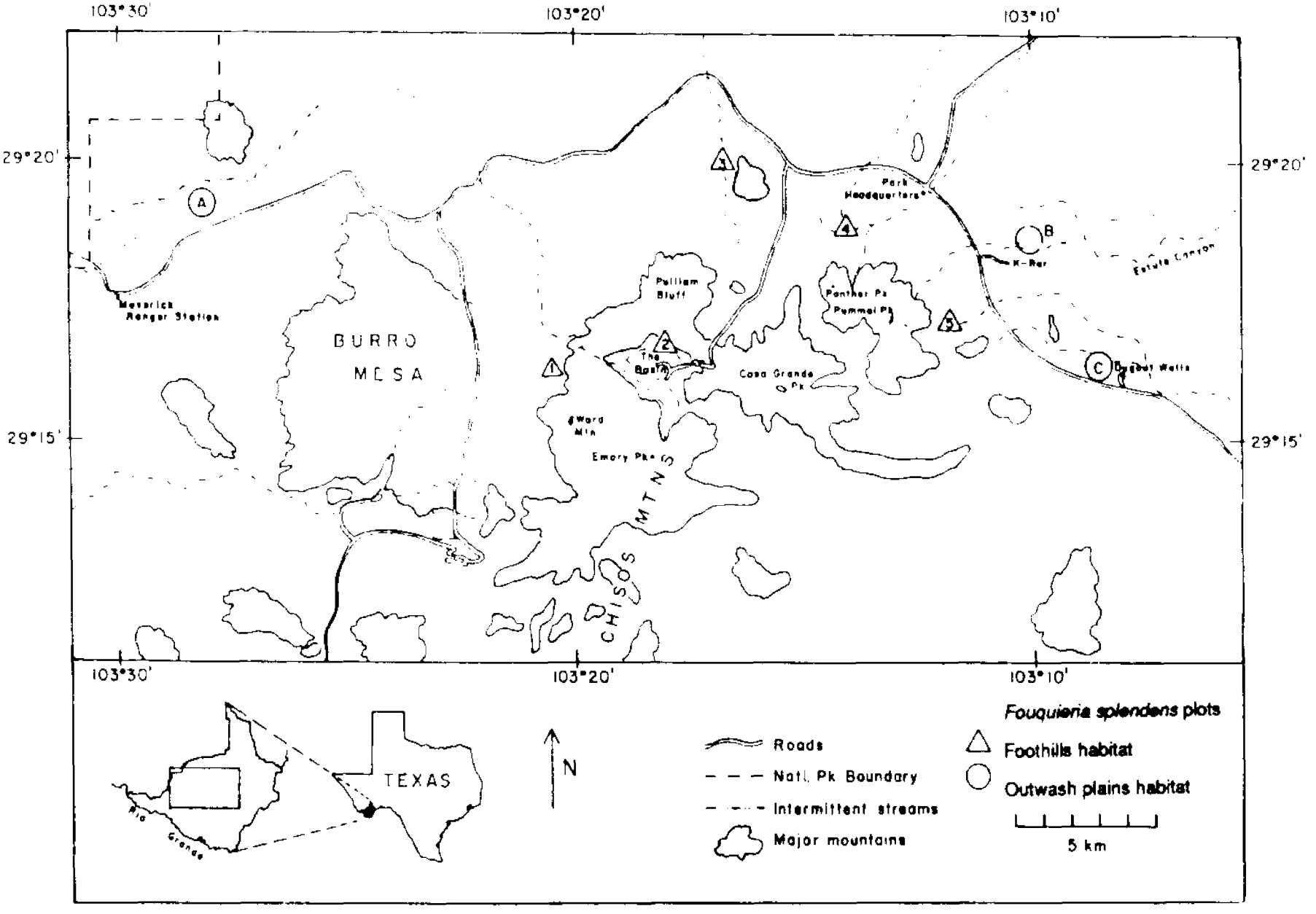
Plant	No. flowers	% Fruit set	Seeds/Fruit $\bar{x} \pm$ S.D. (n)
1	265	23.8	1.5 ± 1.0 (63)
2	68	39.7	2.1 ± 1.6 (27)
3	83	20.5	2.1 ± 1.1 (17)

Table 4.10. Test of breeding system and pollinator limitation in *Fouquieria splendens* at Desert Gardens.

TREATMENT [a]	INFLORESCENCE BAGGED?	FLOWERS SETTING FRUITS %	(N)	SEEDS / FRUIT $\bar{x} \pm$ S.D. (n)	range	SEEDS / FLOWER ($\bar{x}$)
HAND-SELF	YES	5.9	(135)	1.2 ± 0.7 (8)	1-3	0.1
HAND-OUTCROSS (2-4 neighbors)	YES	74.6	(122)	9.8 ± 4.6 (91)	1-18	7.3
ACCESSIBLE TO POLLINATORS	NO	19.2	(192)	2.2 ± 1.8 (37)	1-8	0.4

[a] Treatments replicated on 4 plants, 9-17 March 1988.

Figure 2.1. Map of Big Bend National Park, Texas, showing study sites where *Fouquieria splendens* plants were permanently marked and pollinator visitation rates were quantified. Circles with letters mark sites on the outwash plains: A = Maverick, B = KBar, C = Dugout. Triangles with numbers mark sites in the foothills of the Chisos Mountains: 1 = Cattail, 2 = Basin, 3 = Rough Spring, 4 = Panther Canyon, 5 = Pummel. Elevations and other characteristics are listed in Tables 2.2 and 2.3.


103°30'
103°20'
103°10'
29°20'
29°15'
BURRO
MESA
CHISOS MTNS
Pulliam Bluff
Casa Grande Pk
Emory Pk
Panther Pk
Pummel Pk
Park Headquarters
K-Bar
Estufa Canyon
Maverick Ranger Station
Basin
TEXAS
Rio Grande
N
Roads
Natl. Pk Boundary
Intermittent streams
Major mountains
Fouquieria splendens plots
Foothills habitat
Outwash plains habitat
5 km

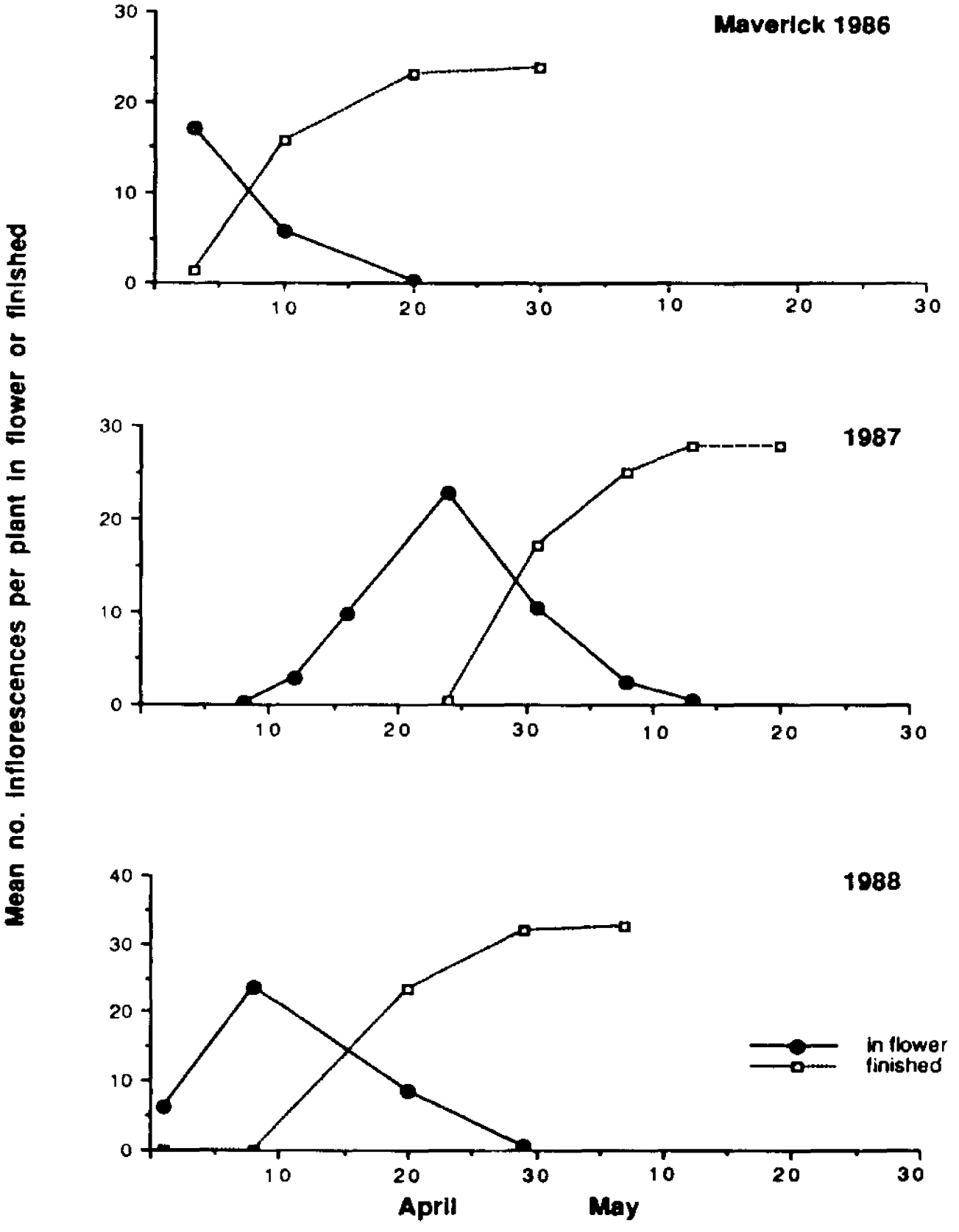


Figure 2.2 a. Timing of flowering in *Fouquieria splendens* at Maverick, Texas (n = 20 plants).

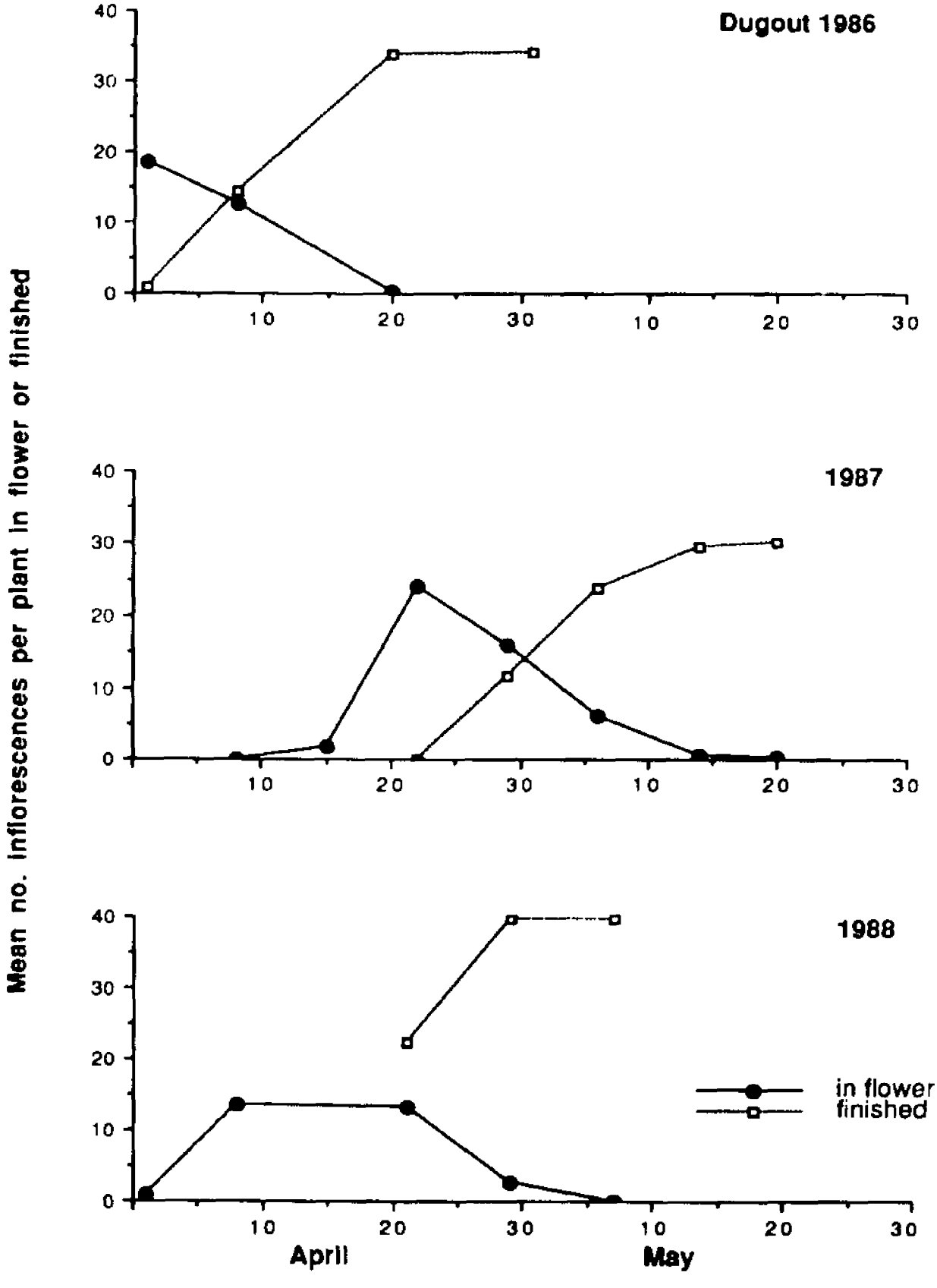


Figure 2.2 b. Timing of flowering in *Fouquieria splendens* at Dugout, Texas (n = 20 plants).

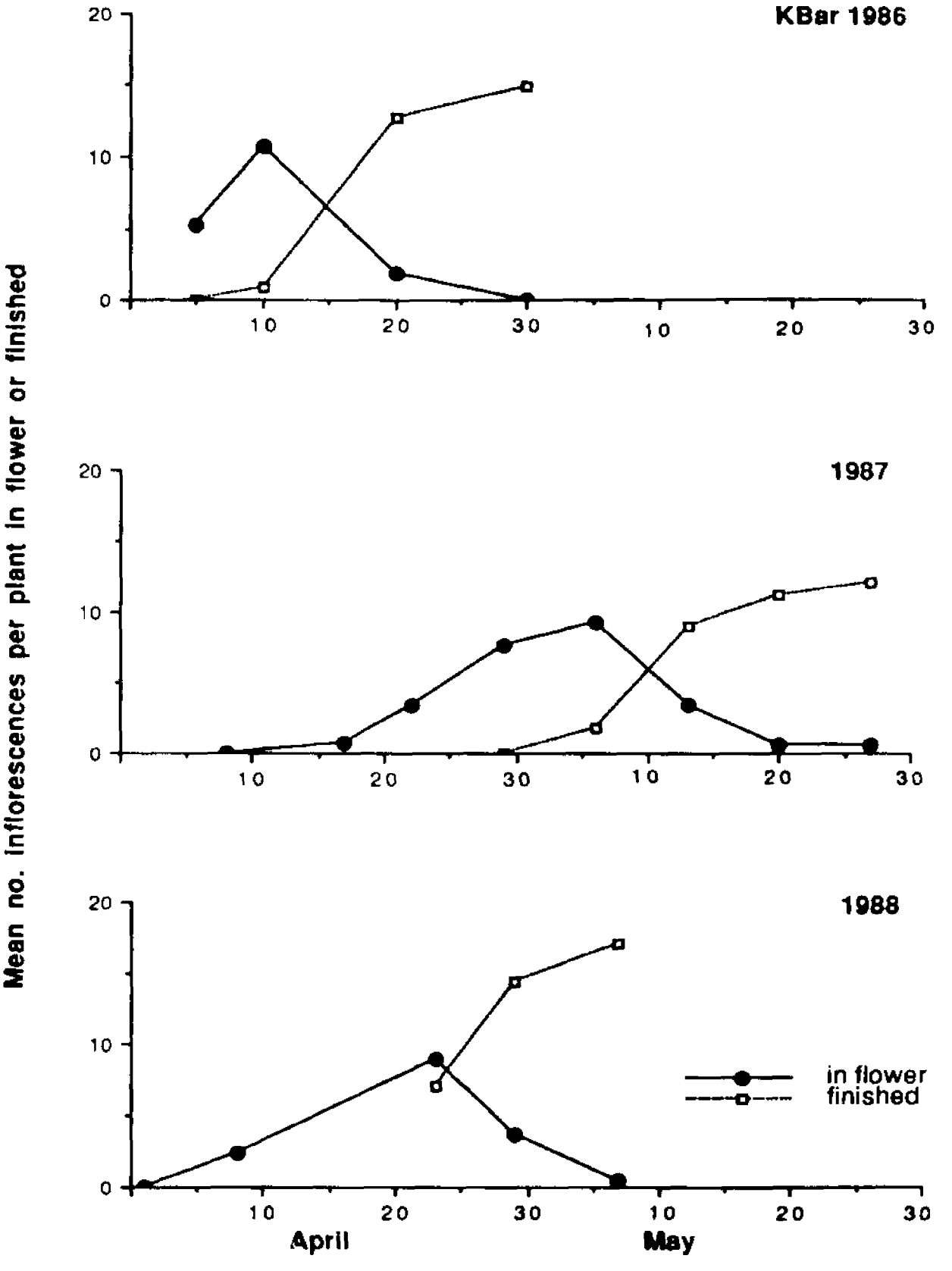


Figure 2.2 c. Timing of flowering in *Fouquieria splendens* at KBar, Texas (n = 20 plants).

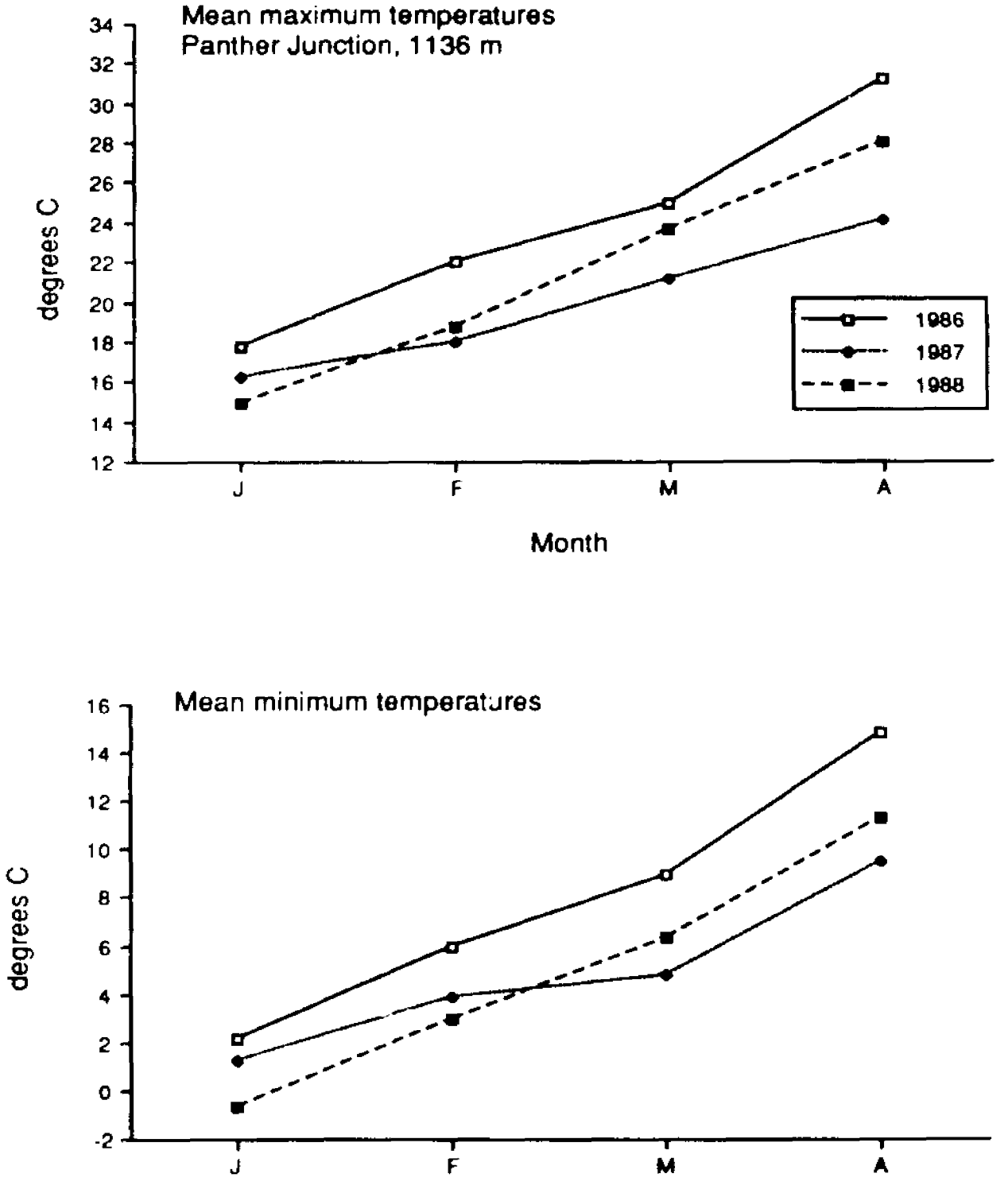
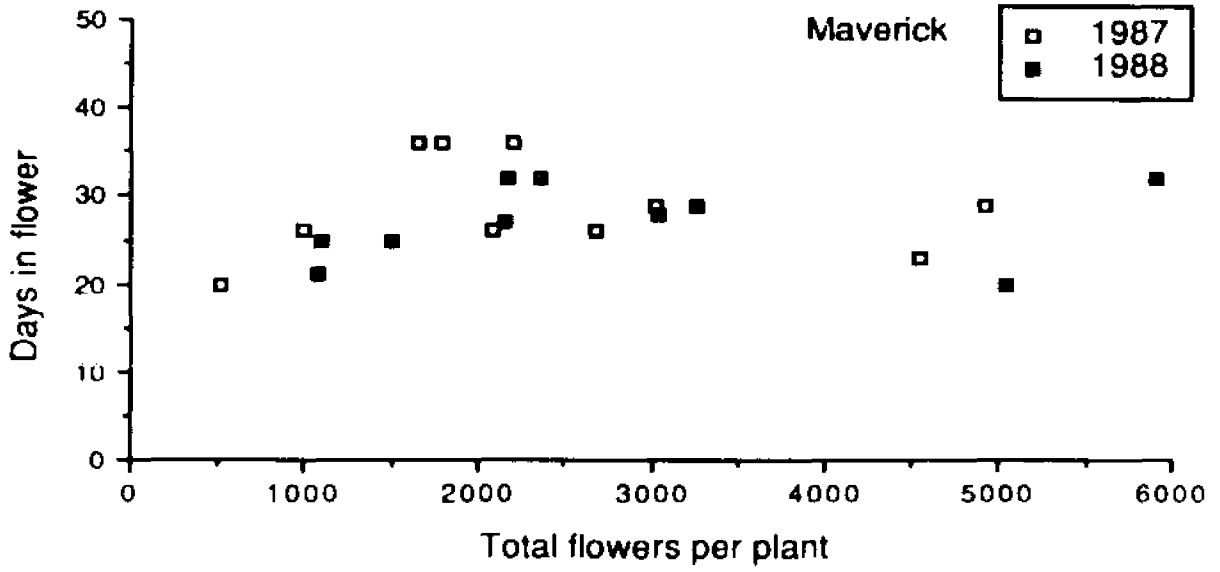


Figure 2.3. Mean monthly temperatures, minimum and maximum, at Panther Junction in January, February, March and April (before and during flowering of *F. splendens*).

Figure 2.4 a-c. The relationship between flower crop size and number of days in flower, or number of flowers opened per day, at Maverick, Dugout, and KBar. Each value is for one plant in a particular year. The linear regression of flowering duration on flower crop size was insignificant ($P > 0.10$), except at KBar in 1987 ($P < 0.01$). The linear regression of number of flowers opened per day on flower crop size was positive for each site and year ($P < 0.001$).


Maverick
1987
1988
Days in flower
Total flowers per plant
0
10
20
30
40
50
0
1000
2000
3000
4000
5000
6000

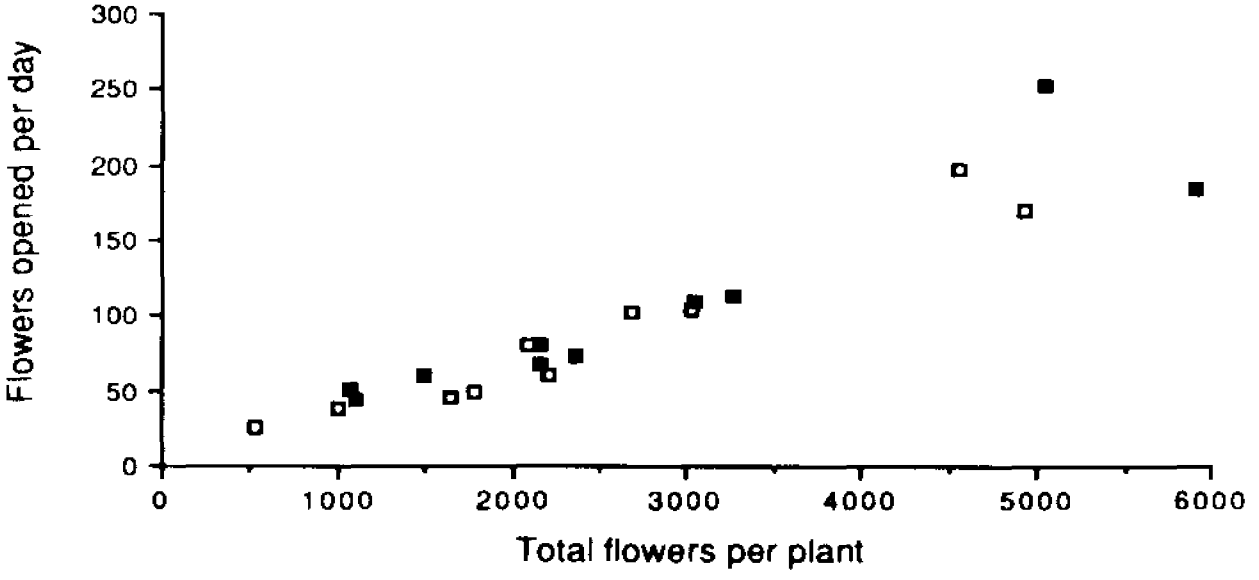

Flowers opened per day
Total flowers per plant
0
50
100
150
200
250
300
0
1000
2000
3000
4000
5000
6000

Figure 2.4 a.

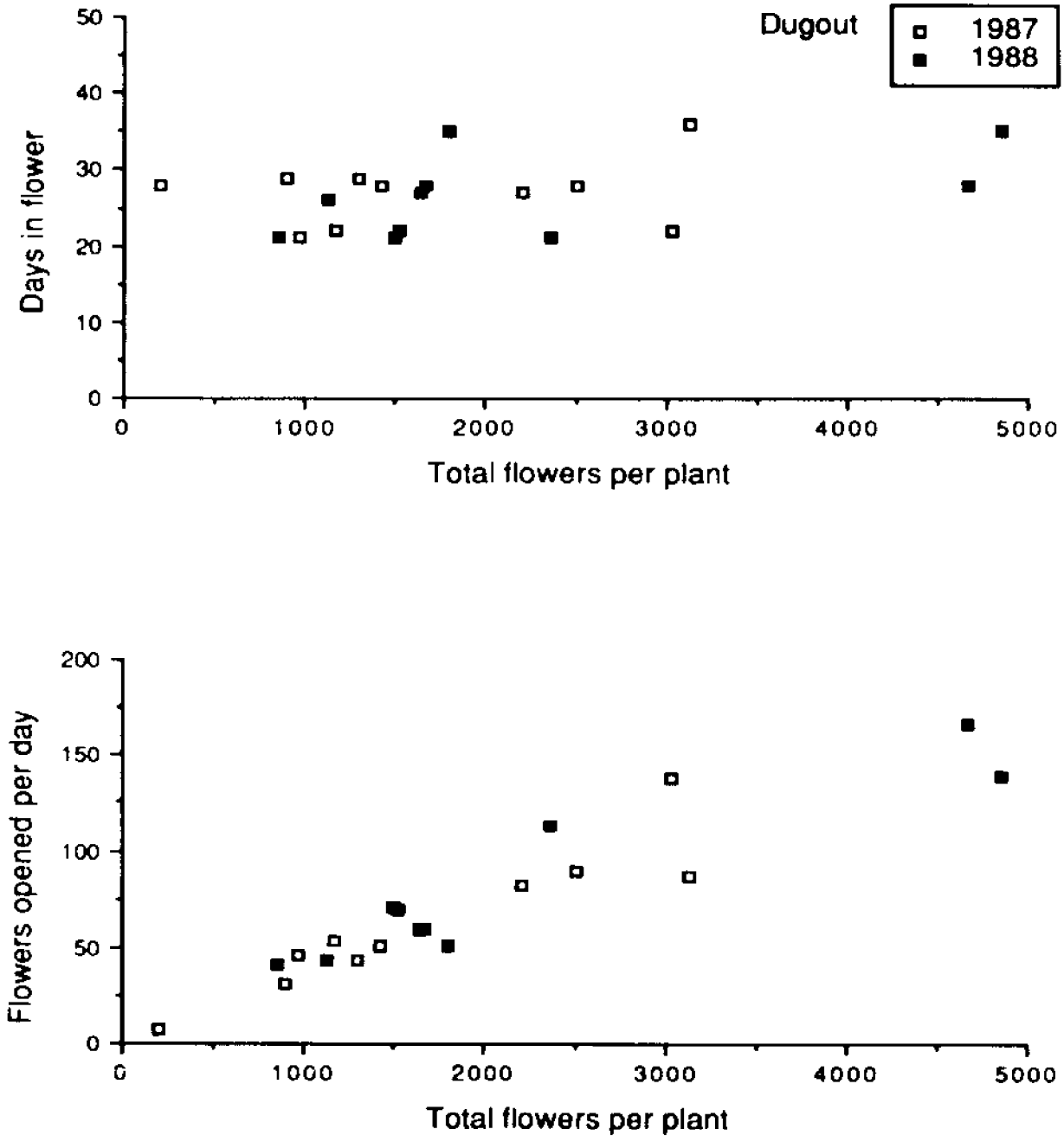
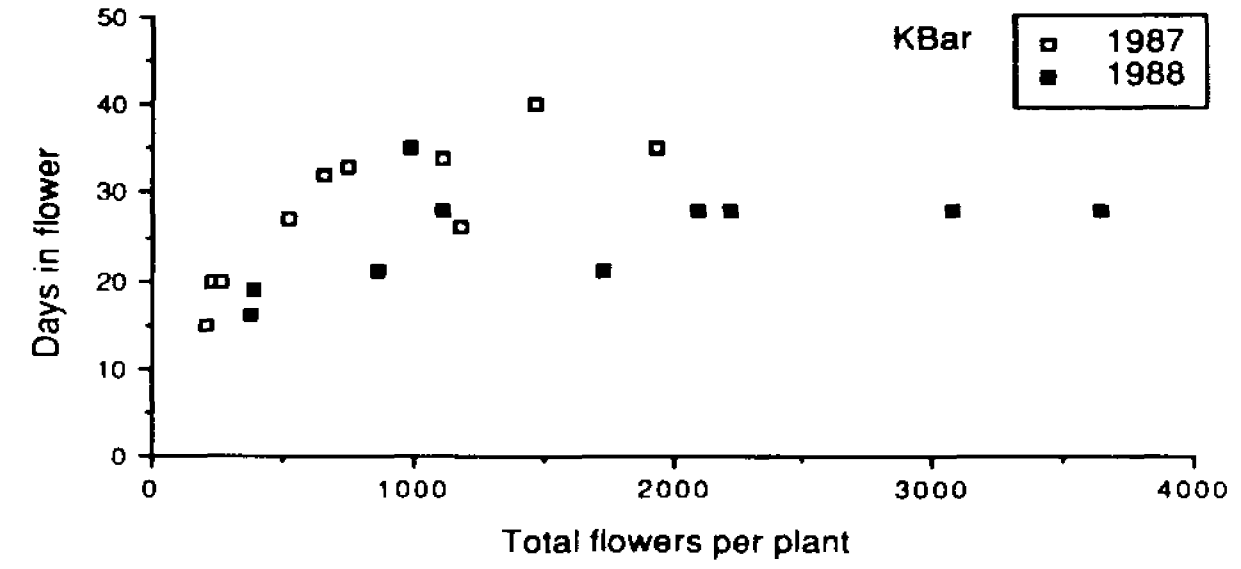

Dugout
1987
1988
Days in flower
Total flowers per plant
Flowers opened per day
Total flowers per plant
0
10
20
30
40
50
0
1000
2000
3000
4000
5000
0
50
100
150
200

Figure 2.4 b.


KBar
1987
1988
Days in flower
Total flowers per plant
0
10
20
30
40
50
0
1000
2000
3000
4000

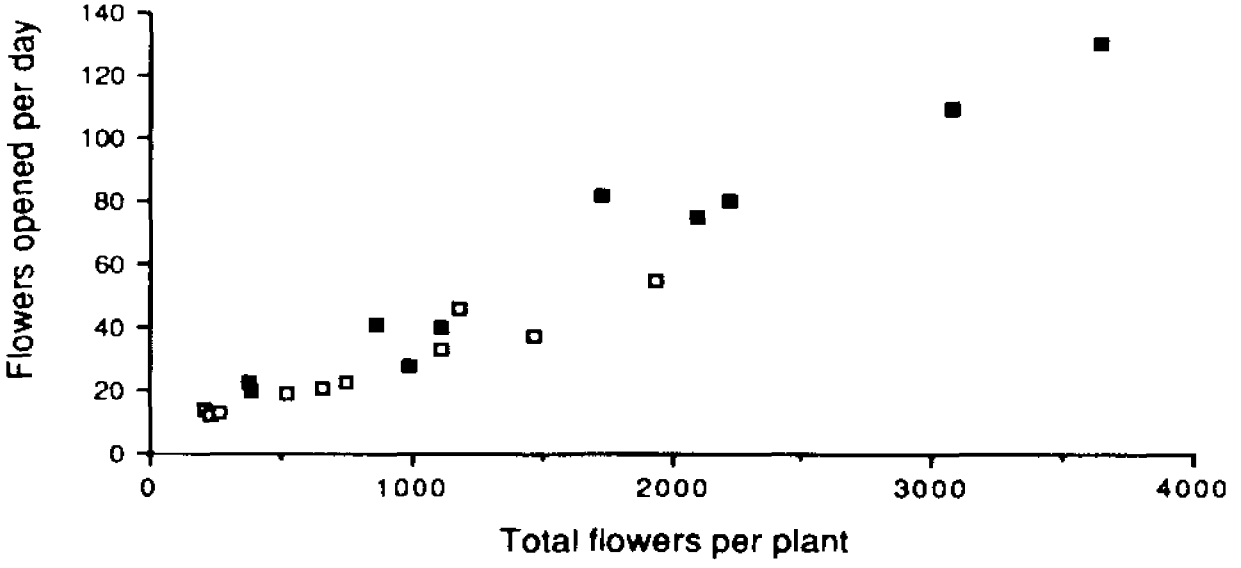

Flowers opened per day
Total flowers per plant
0
20
40
60
80
100
120
140
0
1000
2000
3000
4000

Figure 2.4 c.

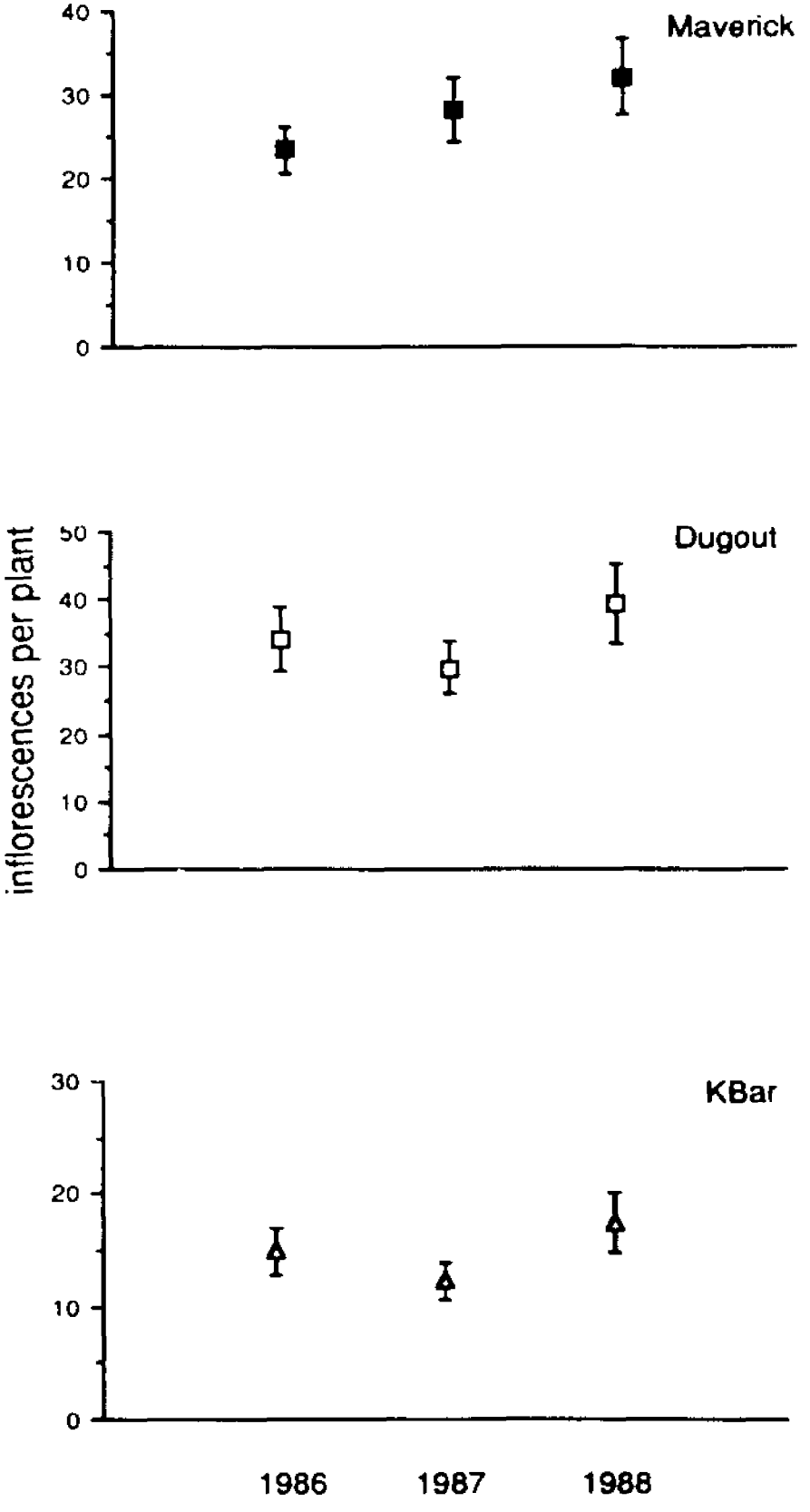


Figure 2.5. The mean number of inflorescences produced by 20 plants at each of 3 sites, 1986-1988. Vertical bars give one standard error of the mean.

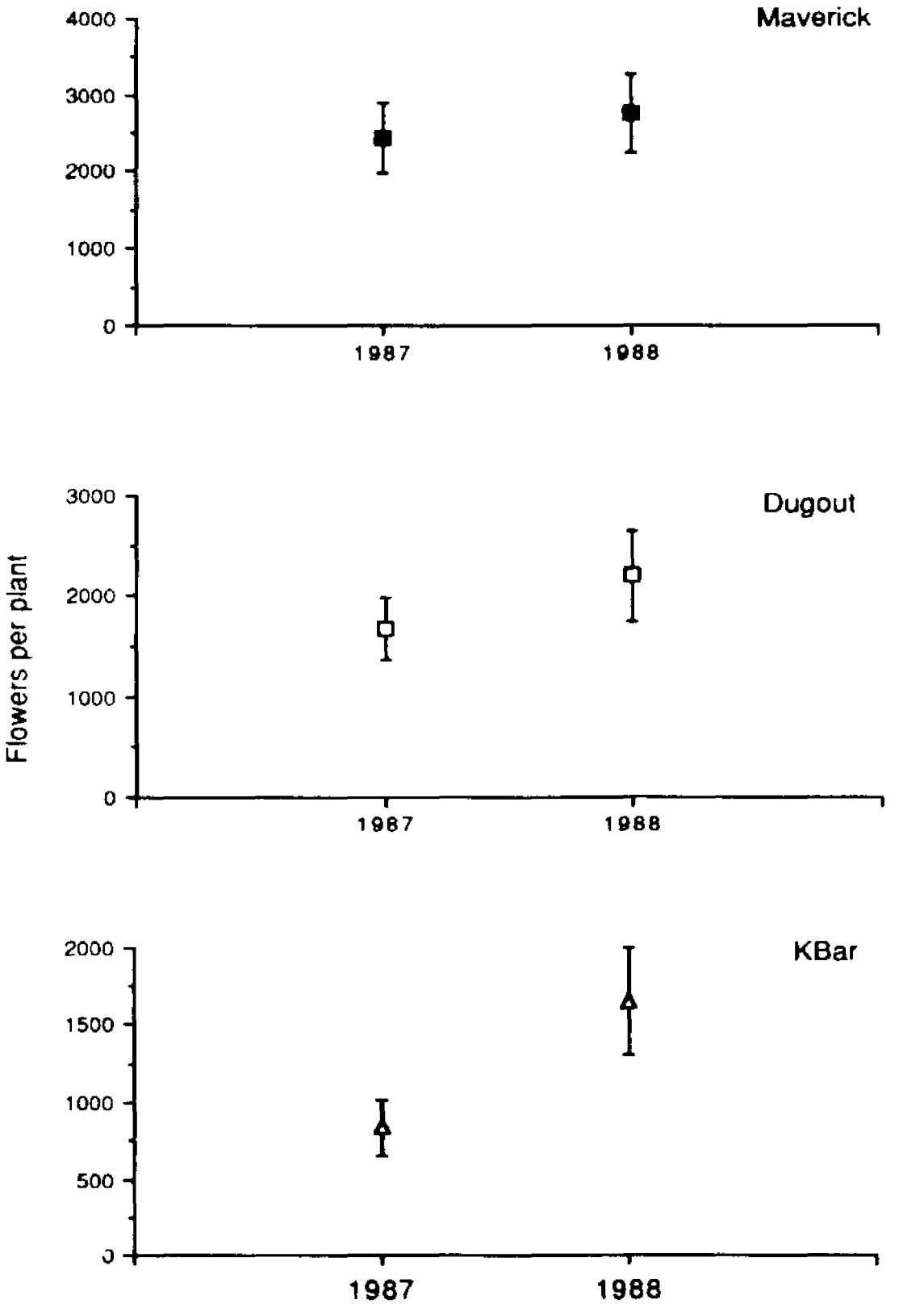


Figure 2.6. The mean number of flowers produced by 10 plants at each of 3 sites, 1987-1988. Vertical bars give one standard error of the mean.

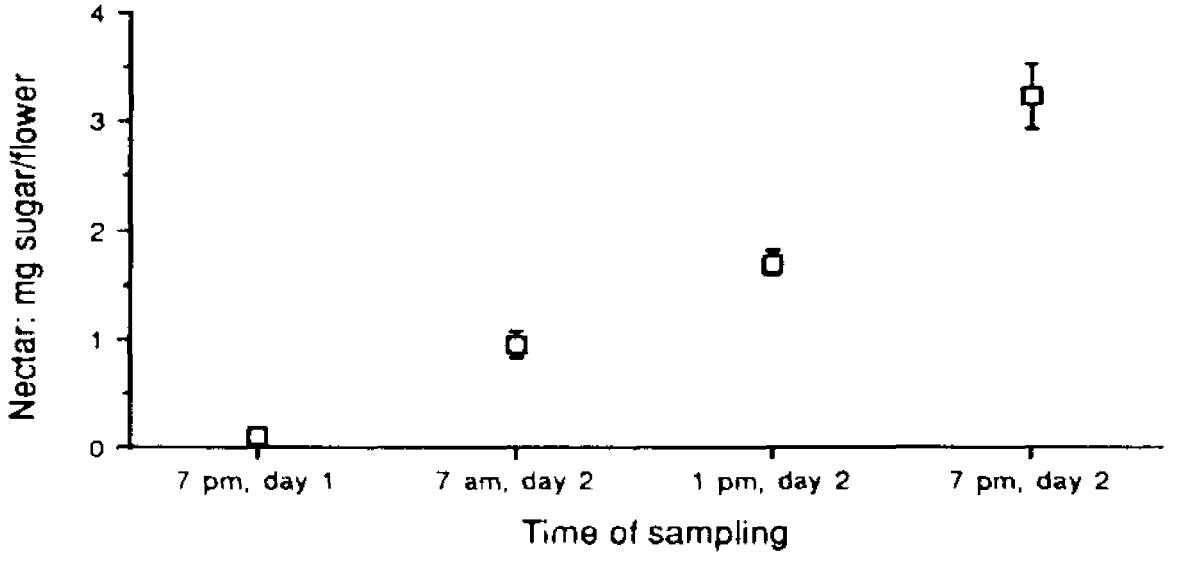


Figure 2.7. Nectar production in *Fouquieria splendens* flowers subsequent to cutting by carpenter bees (Pummel Wash, 21- 22 April 1988). Flowers cut by bees were bagged to prevent further visitation. Nectar was sampled from 6 plants at the time of bagging and 12, 18, and 24 hours later. Squares give sample means; the vertical bars give one standard error of the mean. Sample sizes were 19, 20, 18, and 14 flowers.

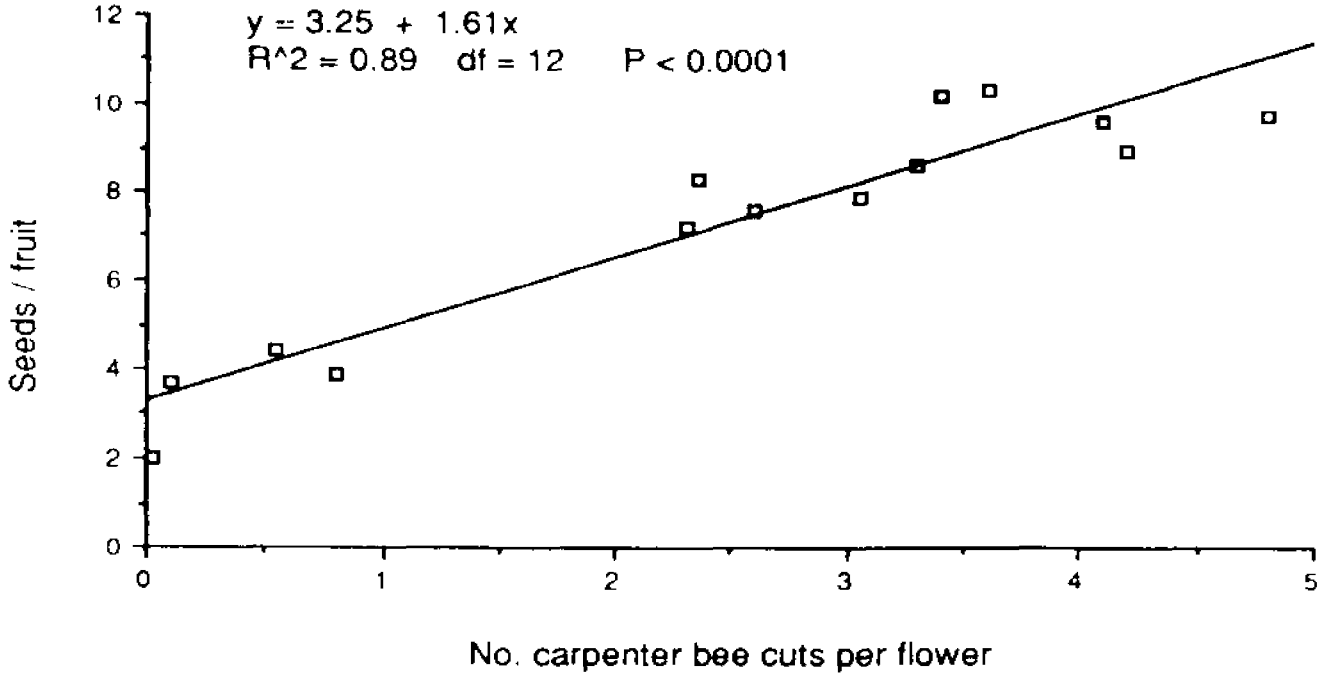


Figure 2.8. Linear regression of *F. splendens* mean seed set on number of carpenter bee cuts per flower. Each point represents mean values for a particular site in one year (see Tables 2.9, 2.12).

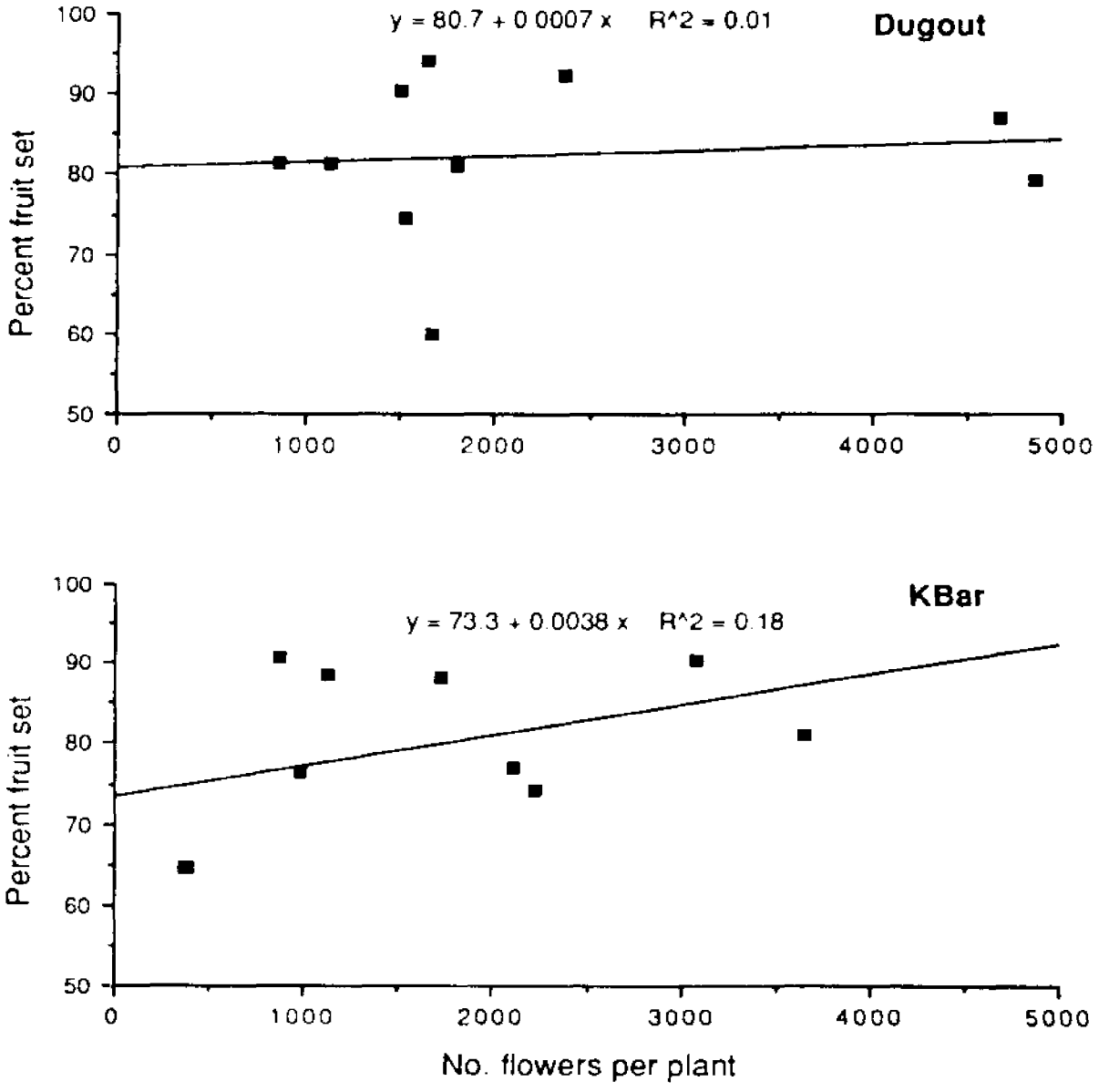


Figure 2.9. The linear regression of percent fruit set on number of flowers produced per plant in 1988. At each site, the slope was not significantly different from zero.

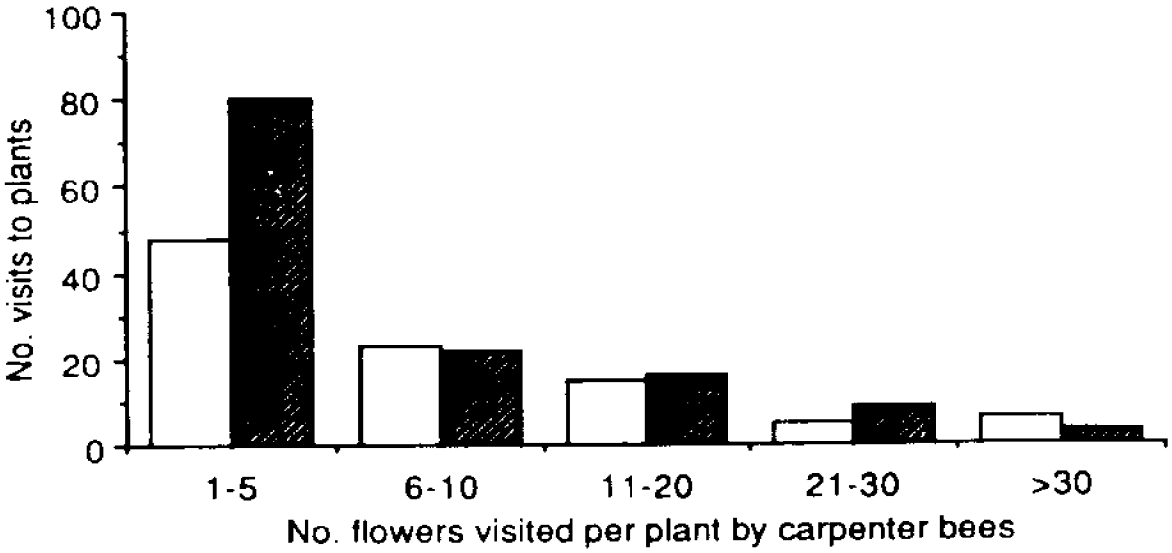
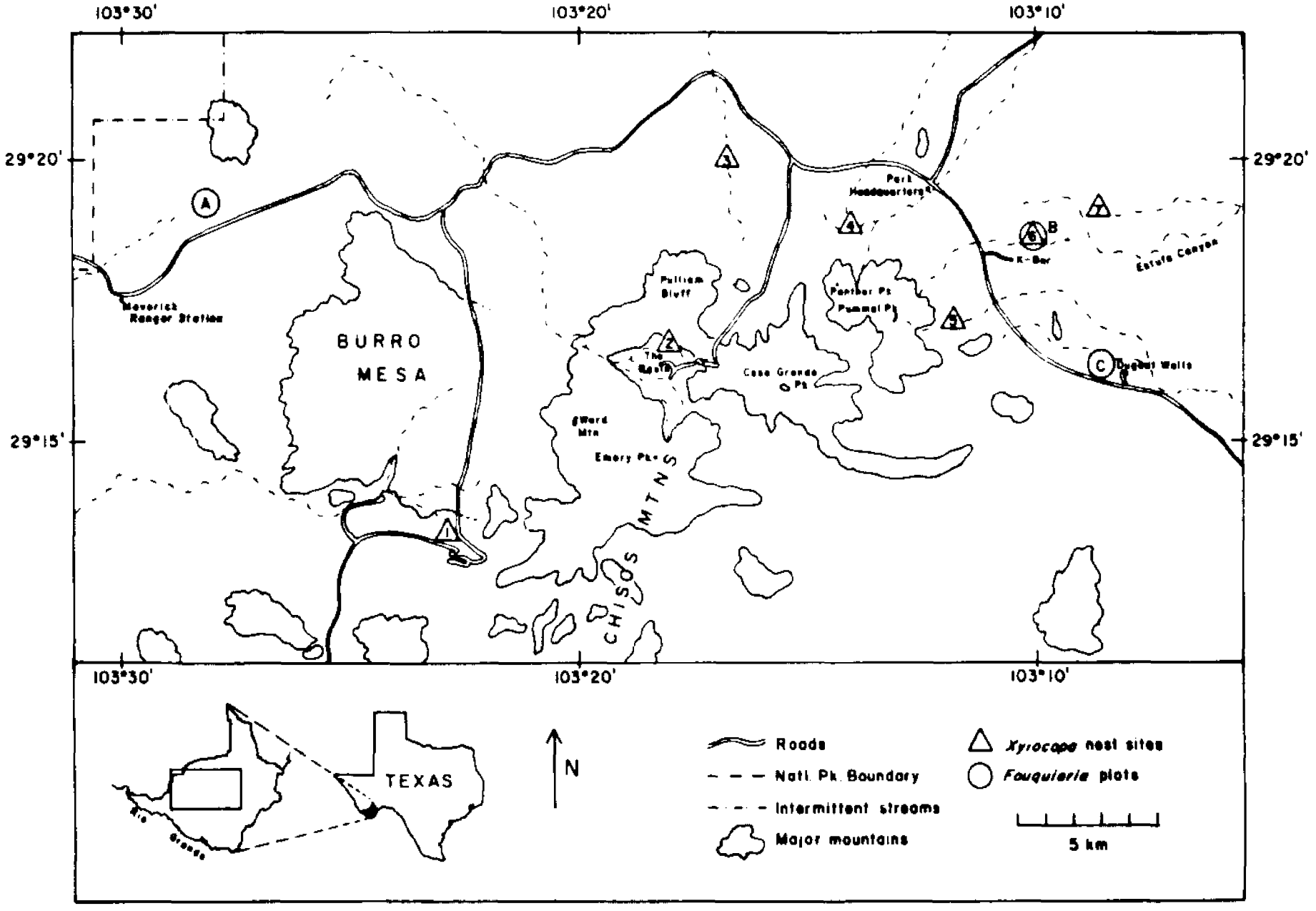


Figure 2.10. Numbers of flowers visited on individual occtillo plants by female carpenter bees in 1988. Data are based on observations of single plants (n = 6; various dates and sites; open columns) or individual bees (n = 12; all at KBar on 26 April; striped columns).

Figure 3.1. Study area in Big Bend National Park, Texas, showing sites where nests of *Xylocopa californica arizonensis* were collected.


103°30'
103°20'
103°10'
29°20'
29°15'
BURRO
MESA
Maverick
Ranger Station
Pulliam
Bluff
Park
Headquarters
Panther Pk
Pummel Pk
Case Grande
Pk
Emory Pk
CHISOS MTNS
K-Bar
Estufa Canyon
Dugout Wells
A
B
C
TEXAS
N
Roads
Natl. Pk. Boundary
Intermittent streams
Major mountains
Xyrocopa nest sites
Fouquieria plots
5 km

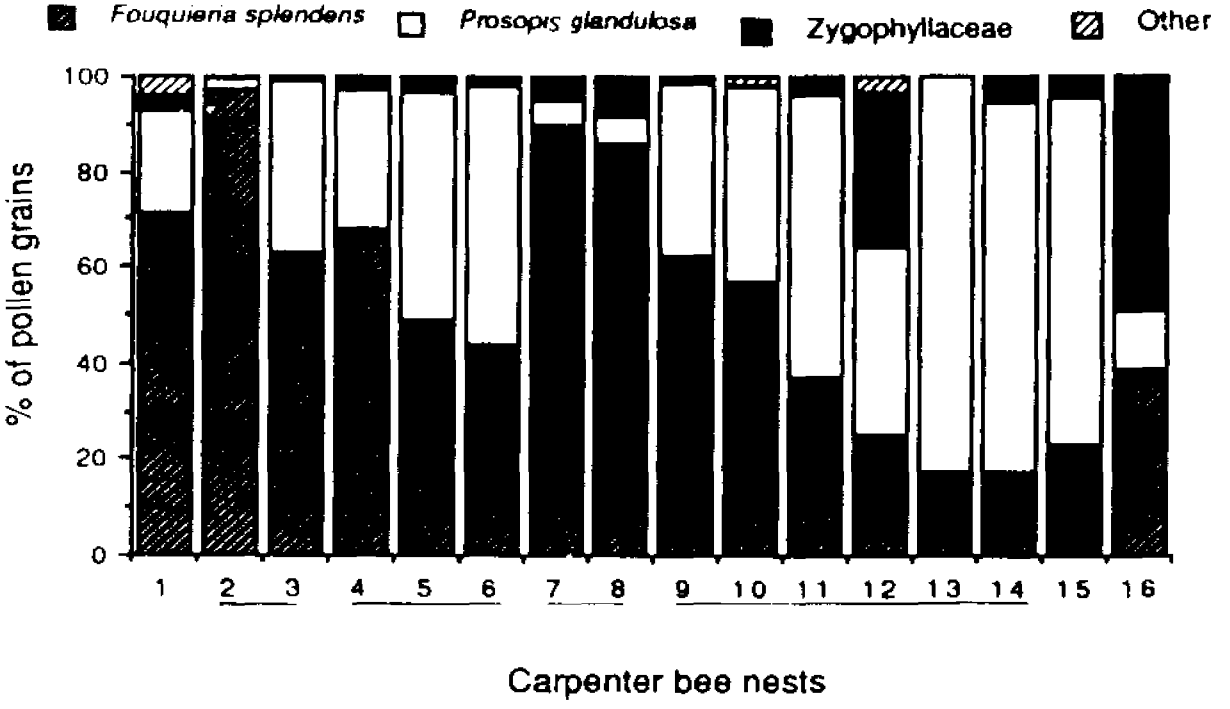


Figure 3.2. The percentages of various pollen types in 500-grain samples from 16 carpenter bee nests, collected at seven sites in spring 1988. Taxa were *Fouquieria splendens*, *Prosopis glandulosa*, Zygophyllaceae (*Larrea tridentata* or *Guaiacum angustifolium*), and "other." Nests from the same site are underlined.

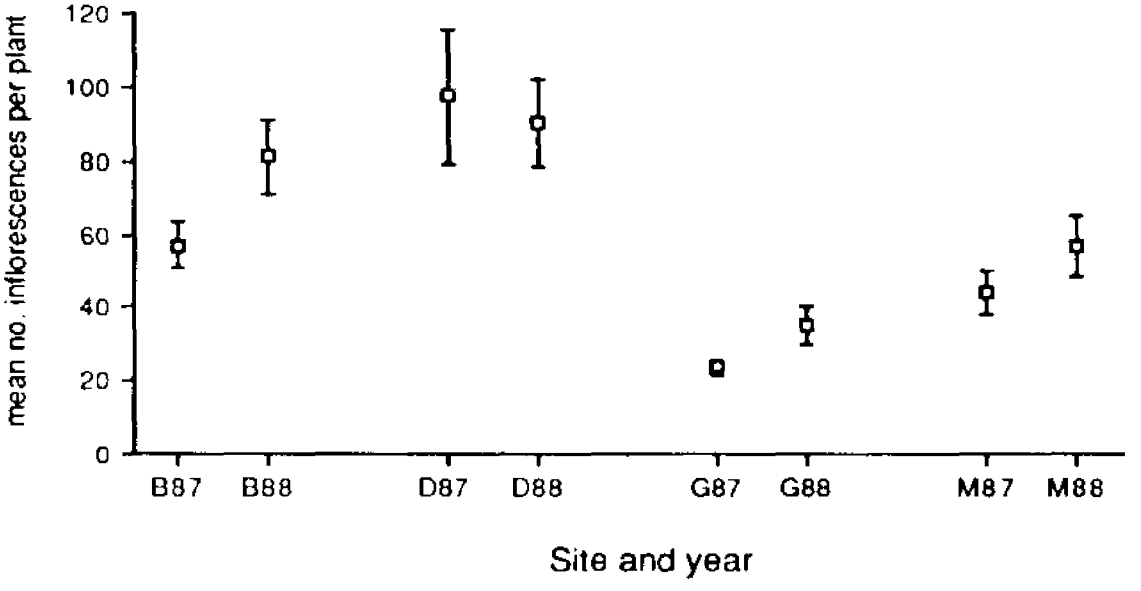


Figure 4.1. Production of inflorescences by California ocotillo plants (n = 20 per site) in 1987 and 1988. Vertical bars give one standard error on either side of the mean (box). Site abbreviations: B = Bow Willow, D = Desert Gardens, G = Glorietta Canyon, M = Mescal Bajada.

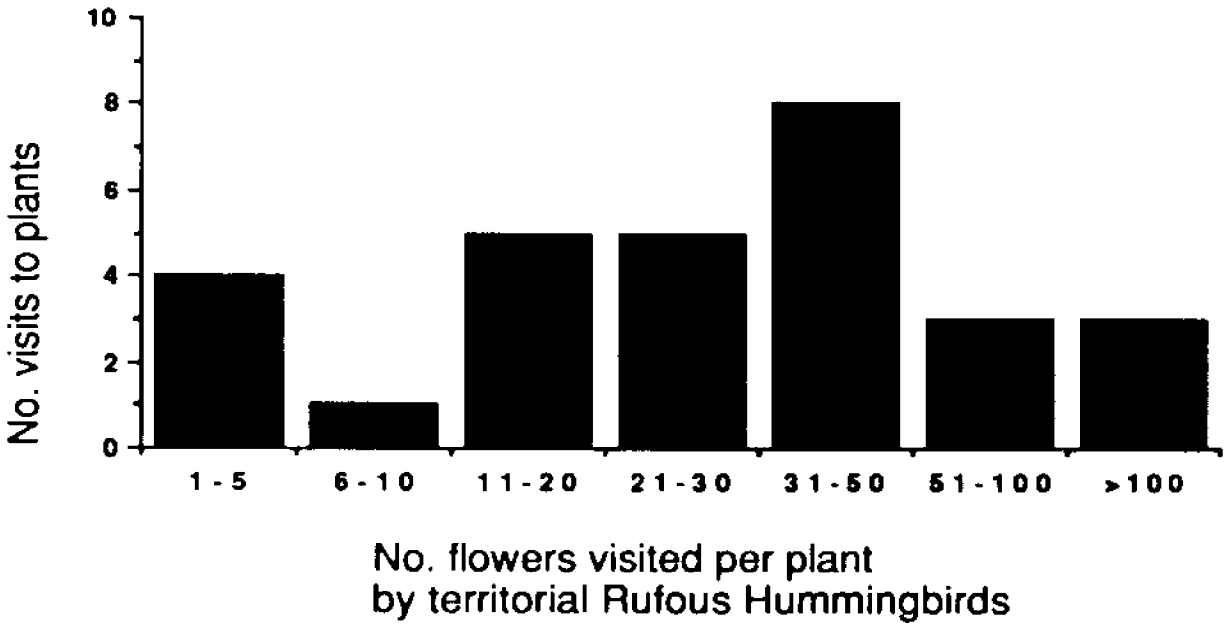


Figure 4.2. Foraging behavior of 3 territorial Rufous Hummingbirds, each observed for 2 hours, at ocotillos at Desert Gardens, California: the number of flowers visited at one plant (including consecutive bouts) before moving to another plant.

VITA

Peter Evans Scott was born on July 6, 1951 in New Haven, Connecticut, the son of Marian Franson Scott and William Evans Scott. He moved with his family to Durham, North Carolina in 1957. After graduating from Durham High School, he entered Yale University in 1969, majored in English, and graduated with honors in 1973. He worked for the National Park Service as a naturalist in Zion National Park, Utah from 1973 to 1976, and in Big Bend National Park, Texas from 1977 to 1979. In 1980 he entered graduate school in the Department of Zoology at the University of Texas at Austin. He received an M. A. in 1984 for a thesis on the reproductive biology of motmots in Yucatan, Mexico. In 1983 he entered graduate school in the Department of Zoology and Physiology at Louisiana State University, where he received the degree of Ph. D. in August 1989.

DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Peter Evans Scott

Major Field: Zoology

Title of Dissertation Ecological consequences of variation in pollinator availability: ocotillo, carpenter bees, and hummingbirds in two deserts

Approved:

Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

Date of Examination:

July 24, 1989